
JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. 57

JANUARY 1976

NUMBER 1

THE GENERA OF CAESALPINIOIDEAE (LEGUMINOSAE)
IN THE SOUTHEASTERN UNITED STATES¹

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Subfamily CAESALPINIOIDEAE A. P. de Candolle, Prodrromus
2: *tab.* inter 94 & 95, 473. 1825, "Caesalpinieae"

(CAESALPINIA SUBFAMILY)

Trees, shrubs, perennial or annual herbs, or (infrequently) lianas; in tribe Caesalpinieae plants often armed. Leaves alternate, persistent or deciduous, compound, even- [or odd-]pinnate or bipinnate, rarely ap-

¹ Prepared for the Generic Flora of the Southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant BMS74-21469, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. 39: 296-346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on plants in this area, with additional information from extraterritorial taxa in brackets. References that we have not seen are marked by an asterisk.

The treatments of *Gymnocladus* and *Gleditsia* are largely by Y. T. Lee, who prepared them while he was a Mercer Fellow of the Arnold Arboretum. The subfamily discussion and the treatments of the remaining genera are by K. R. Robertson. For the treatment of subfamily Mimosoideae, see T. S. Elias, Jour. Arnold Arb. 55: 67-118. 1974.

Both plates of *Caesalpinia* and that of *Gymnocladus* were drawn by Karen S. Velmure; the plates of *Cercis* and *Cassia* are by Arnold D. Clapman; figures *a* and *e* of the *Gleditsia* illustration are by Sue Sargent, with the remaining figures by Arnold D. Clapman. Living and/or alcohol-preserved materials for these illustrations were collected by D. F. Austin, G. R. Cooley, T. S. Elias, W. T. Gillis, F. Harper, R. A. Howard, Y. T. Lee, K. R. Robertson, and C. E. Wood, Jr.

Professor Wood has freely given his critique and has continued to share his enormous knowledge of plants; his assistance is sincerely appreciated. Kathleen Clagett has given much editorial advice. Dr. Annetta Carter, University of California, Berkeley, kindly reviewed the treatment of *Parkinsonia* and has given permission to quote from her recent article on *Cercidium*. Considerable assistance has been given by R. M. Parkhurst, Stanford Research Institute, Menlo Park, California, on the saponin chemistry of *Gymnocladus* and *Gleditsia*. The manuscript was typed by Beverly Vincent.

pearing simple [or unifoliolate or absent], petiolate; foliar glands on petiole or rachis present only in *Cassia*; pinnae and leaflets opposite or infrequently alternate; leaflets large to small, few to numerous or reduced and the rachis phyllodial, usually with entire margins, sometimes with pellucid dots; petioles, pinnae, and leaflets usually with a basal pulvinus; stipules paired, small to foliose or spinescent, caducous or persistent; stipels absent or rarely present and minute. Inflorescences terminal and/or axillary racemes, panicles, or spikes, sometimes reduced to subumbels or fascicles or the flowers solitary, sometimes cauliflorous; pedicels occasionally jointed; bracts usually present, small to conspicuous [or sepaloid], caducous to persistent. Flowers large to moderately small, often showy, usually bilaterally symmetrical, not papilionaceous (except in *Cercis*), yellow to pink, red, or purple, rarely or never blue, usually 5-merous except for gynoeceium, perfect (or rarely imperfect in tribe Caesalpinieae and the plants then polygamous to dioecious). Sepals usually imbricate in aestivation, rarely valvate, the adaxial one sometimes cucullate, \pm connate below into a short to long cup or tube [or free], sometimes also adnate to the receptacle and bases of the filaments and petals, forming a short to long floral cup or tube, the calyx lobes small to petaloid, \pm equal to strongly unequal [rarely the entire calyx connate in bud and splitting irregularly as the flower opens]. Petals ascending-imbricate in bud, with the adaxial petal innermost and covered by the lateral ones, usually 5 [sometimes reduced to 4 or 1 or absent], free [or connate below], \pm equal to strongly unequal, one petal often different from the others. Androeceium usually bilaterally symmetrical and composed of 10 mostly unequal stamens in 2 whorls, rarely fewer [or numerous], all fertile or some reduced to staminodia; filaments short to greatly elongated, free to base or partly united [rarely diadelphous], often curving toward center of flower, usually pubescent at base; anthers dehiscing by longitudinal slits or apical [or basal] pores or slits, basifixed to dorsifixed, often versatile, lacking apical glands; pollen grains usually shed singly. Gynoeceium of one sessile or stipitate carpel (except in abnormal flowers) inserted at base of floral or calyx cup or the gynophore adnate to the floral tube; ovary superior; style short to elongate, often curving adaxially; stigmatic area terminal, rarely oblique, small to dilated [or petaloid]; ovules anatropous, parietal, few to numerous in 2 rows on either side of the adaxial suture. Fruits very variable, stipitate or not, usually elongate [rarely globose], cylindrical to laterally compressed or flattened, straight or curved, sometimes winged, indehiscent, irregularly dehiscent, or dehiscent (sometimes elastically) along one or both sutures; externally constricted or not [or lomentlike], internally septate or not, with or without pulp; fruit walls chartaceous to woody or fleshy, glabrous to pubescent or echinate. Seeds large to rather small, \pm globose to ovoid, rhomboid, or variously flattened, oriented transversely, obliquely, or longitudinally in the fruit, the hilum apical or subapical, small; seed coat usually very hard, variously marked, a closed pleurogram present in a few genera, but U-shaped pleurograms absent (cf. Mimosoideae); funiculus usually rather long; endosperm

abundant to lacking; embryo usually large, with large, flat cotyledons; radicle superior, short, thick, straight.

The Caesalpinioideae, one of three generally recognized subfamilies of Leguminosae (Fabaceae), includes 120 to 180 genera and 1500 to 3000 species, mostly of the tropics and subtropics. The subfamily is most diverse in both wet and dry areas of tropical America and tropical Africa, although few genera occur in both hemispheres. A smaller number of genera occur in tropical Asia, with relatively few genera in Polynesia, Australia, and the temperate regions of North and South America and Eurasia. Only a few genera (including *Cercis*, *Gymnocladus*, *Gleditsia*, and *Ceratonia* L.) are largely confined to temperate regions. Most genera of the subfamily are small, and, of the 152 genera (not including those of tribe Swartzieae) accepted by Hutchinson in his relatively conservative account (in which *Bauhinia* L., *Cassia*, and *Caesalpinia* are interpreted broadly), 62 are monotypic and 38 have from two to five species. In the broad sense, *Cassia* and *Bauhinia* are by far the largest genera, with about 600 and 570 species respectively; few, if any, of the other genera have more than 100 species.

There is general agreement that the three subfamilies that comprise the family Leguminosae, the Mimosoideae, Caesalpinioideae, and Faboideae,² are natural assemblages. There are differences of opinion, however, concerning the rank to be assigned to these taxa. Takhtajan and Hutchinson treat each as a family, i.e., the Mimosaceae, Caesalpinaceae, and Fabaceae, of the order Fabales or Leguminales. Hutchinson (1964, p. 223) has said that "it is merely a matter of opinion or convenience (or even of prejudice!) whether Caesalpinaceae should be treated as a separate family from Mimosaceae and Fabaceae (Papilionaceae) or all three regarded as subfamilies of Leguminosae." However, the distinguishing characters of the three taxa break down to such a degree that it seems far better to keep them at the rank of subfamily.

The subfamilial classification often used today follows that established by Bentham, with some modifications; see Heywood in Harborne *et al.* for a discussion of the classification of the subfamily and a very useful enumeration of the genera of Caesalpinioideae arranged alphabetically by tribes. The eight tribes of Caesalpinioideae usually recognized are Dimorphandreae Bentham (9 genera), Caesalpinieae Endl. (28 genera), Cassieae Bronn (20 genera), Detarieae DC. (Cynometreae Bentham emend. J. Léonard, 52 genera), Amherstieae Bentham emend. J. Léonard (33 genera), Cercideae Bronn (Bauhinieae Bentham, 11 genera; *Bauhinia* sensu lato, divided into 10 genera), Sclerolobieae Bentham (12 genera),

² The names Lotoideae and Papilionoideae have also been used for this subfamily. According to Article 19 of the *International Code of Botanical Nomenclature* (1969), the name of a subfamily that includes the type genus of a family must be based on the name of that genus. Since *Faba* Miller (= *Vicia* L.) is the type genus of the Leguminosae, the correct name for this subfamily is Faboideae. The name Papilionoideae cannot be used under any circumstance.

and Swartzieae DC. (11 genera) (sequence that of Brenan, 1967; number of genera from Heywood in Harborne *et al.*). *Amphimas* Pierre ex Harms (four species of tropical West Africa) was placed by Bentham in tribe Cadieae of subfam. Faboideae, but has been included by Schulze-Menz in the Caesalpinioideae as the sole genus of tribe Amphimanteae Pellegrin. Hutchinson considers the differences between Bentham's tribes to be slight and divides his family Caesalpinaceae into two subfamilies, the Brachystegioideae (largely equivalent to tribe Amherstieae as emended by Léonard), with the calyx reduced and functionally replaced by sepaloid bracteoles, and the Caesalpinioideae, which was subdivided into five artificial groups. The systematic disposition of *Swartzia* and related genera is debatable. They have been considered to compose a tribe of subfam. Faboideae (Bentham) or of family Fabaceae (Hutchinson), a tribe of subfam. Caesalpinioideae (Taubert, Airy Shaw in Willis, Schulze-Menz, Brenan), or a distinct subfamily (De Candolle, Corner). *Krameria* L., sometimes assigned to the Caesalpinioideae, seems better placed in its own family (see K. R. Robertson).

Tribe Dimorphandreae (flowers small, mostly regular; stamens 10, in two whorls of alternating lengths, but usually otherwise uniform) approaches tribe Parkieae of subfam. Mimosoideae, and tribe Swartzieae (flowers nearly regular to irregular; calyx completely synsepalous in bud, splitting irregularly as the flowers open; embryo with a straight or curved radicle) is close to tribes Cadieae and Sophoreae of subfam. Faboideae.

In traditional systems of classification of Leguminosae, the sequence of the subfamilies, reflecting increasing morphological complexity, is (1) Mimosoideae, (2) Caesalpinioideae, and (3) Faboideae. Today, however, most phylogenists agree that the subfamily Caesalpinioideae is the least specialized and that it is linked through tribe Dimorphandreae to the Mimosoideae and through tribe Swartzieae to the Faboideae. Turner & Fearing proposed a hypothetical phyletic chart of the Caesalpinioideae and Faboideae based mainly on chromosome numbers. The tribes of Caesalpinioideae were considered to comprise three basic stocks: Amherstieae, in part ($x = 12, 14$), and "Eucaesalpinieae" ($x = 12, 14$); Bauhinieae ($x = 7$) and Cassieae ($x = 7$, with $x = 8$ secondary in *Cassia*); and Amherstieae, in part ($x = 8$), Cynometreae, in part ($x = 8, 10$), Sclerolobieae ($x = 11$), and Swartzieae ($x = 8$). According to Turner & Fearing, the Faboideae may be polyphyletic in origin from the last group of caesalpinoid tribes. Leguminosae, Chrysobalanaceae, and Rosaceae are sometimes included within the same order, and Hutchinson regards the caesalpinoid genera *Bandeiraea* Welw. ex Bentham & Hooker and *Bauhinia* to be connecting links between his Caesalpinaceae and his tribe Chrysobalaneae of the Rosaceae (often separated as Chrysobalanaeae; see Prance, Jour. Arnold Arb. 51: 522. 1970). Takhtajan says that his order Fabales (= Leguminosae in this paper) is "close to the Saxifragales and evidently derived from their immediate ancestor."

Like most primarily tropical and subtropical plant groups, the subfamily Caesalpinioideae is not very well known cytologically. Reported

sporophytic chromosome numbers (arranged by tribes) are Dimorphandreae, 24, 28; Caesalpinieae, 22, 24, 26, 28; Cassieae, 14, 16, 20, 22, 24, 26, 28, 32, 48, 56, 64; Detarieae (Cynometreae), 12, 16, 20, 22, 24, 36, 48; Amherstieae, 24, 28; Cercideae, 14, 28, 42; Sclerobieae, 22; Amphimanteae, 22; and Swartzieae, 16, 20 (data mostly from Heywood in Harborne *et al.*). Most genera and species counted thus far have derived, polyploid base chromosome numbers of 12, 13, or 14. Very few species are reported as diploid, with base numbers of 6 (*Sindora siamensis* Teysm. ex Miq.), 7 (*Cercis canadensis*, *C. occidentalis*, *C. Siliquastrum*, *Cassia* sect. CHAMAECRISTA subsect. XEROCALYX), and 8 (*Sindora Supa* Merrill, *Trachylobium verrucosum* Oliver, *Swartzia madagascariensis* Desv., *Cassia* sect. CHAMAECRISTA subsect. LEIOCALYX). A base number of 8 has been reported in four tribes, although it is never common. Turner & Fearing postulate that "in view of the distribution of the $2n = 16$ diploid species in the family, particularly in the Caesalpinioideae, it seems most likely that 8 represents the original basal number for the Leguminosae, if such numerical archetypes exist. At a very early time, derived aneuploid lines of $x = 7$ might have given rise to the Bauhinieae and perhaps other $x = 14$ groups in the Caesalpinioideae as well as derived secondary aneuploids at the higher level of $x = 12$ and 13, but the major flow of the $x = 8$ line appears to have gone into the production of the Papilionoideae proper." The occurrence of somatic polyploid or aneuploid variant nuclei in root tip tissue has been noted in numerous genera of Caesalpinioideae and Mimosoideae, but not in genera of Faboideae (see Berger *et al.*, Sharma & Raju, and Turner & Fearing).

The pollen grains of most Caesalpinioideae are shed singly (Erdtman reports that the pollen of *Afzelia africana* Pers. remains in tetrads) and are nearly always 3-colporate (rarely appearing 3-porate), with narrow to broad, sometimes equatorially constricted, mostly elongate colpi and circular, lalongate, or infrequently lolongate ora. The shape of the grains in equatorial view is spheroidal, prolate, or oblate (infrequently flattened equatorially) and in polar view circular, 3-angled, or triangular. The exine is quite variable, both within and between genera, and may be smooth, punctate, rugulose, striate, reticulate, or verrucose. Considering the diversity of exine patterns in the species studied thus far, it would seem that a comprehensive survey of the subfamily with the use of the scanning electron microscope would be worthwhile, particularly for the larger genera.

Very little biological information about the genera of Caesalpinioideae is available, but the extraordinary diversity of flower and fruit structure indicates an equal diversity in the reproductive biology. There are few published accounts of pollinators of the Caesalpinioideae, but it seems that most species are pollinated by various diurnal insects. Some species of *Bauhinia*, *Eperua* Aublet, and *Hymenaea* L. are bat pollinated, and species of *Hardwickia* Roxb. are reportedly wind pollinated. Large black ants, hummingbirds, and bats visit the flowers of *Eperua rubiginosa* Miq., although it is not known what role each of these animals plays in the

actual pollination of this species (see Cowan, p. 15). Numerous floral modifications presumably linked to pollination occur in the subfamily, suggesting that detailed studies of floral biology would be worthwhile. (*Bauhinia* is particularly variable in this respect.)

The gynoecium of virtually all Caesalpinioideae consists of a single carpel that, by and large, is not too different in the various tribes and genera. Yet the diversity of fruit types in the subfamily is remarkable. Because of this variety (see subfamily description), the term "legume" is probably defined best as the fruit of members of the Leguminosae, although it is usually defined as a dry unilocular fruit that dehisces along both sutures.

Concomitant with the diverse morphology of the fruits are a number of dispersal mechanisms. Some selected examples follow. (The inclusion of a genus in one category does not necessarily imply that all species of that genus have the same mode of dispersal.) The fleshy or pulpy fruits of species of *Cassia*, *Ceratonia*, *Detarium* Juss., *Dialium* L., *Gleditsia*, *Gymnocladus*, *Hymenaea*, and *Tamarindus* are dispersed mostly by bats or arboreal or ground-dwelling mammals. Arils or arilloids are present in species of *Afzelia* Sm., *Copaijera* L., *Sindora* Miq., and *Swartzia* Schreber, and the seeds are largely dispersed by birds. Explosively dehiscent fruits are found in species of *Bauhinia*, *Brachystegia* Benth, *Caesalpinia*, *Cassia*, *Delonix*, and *Eperua*. Winged or strongly flattened fruits dispersed by wind occur in species of *Burkea* Benth, *Cercis*, *Daniellia* J. Benn. (endocarp winged), *Gleditsia*, and *Pterolobium* Wight & Arnott; in *Melanoxylon Brauna* Schott the seeds are winged. The fruits of *Gleditsia aquatica* and *Cynometra ramiflora* L. float and are transported by water; the seeds of *Caesalpinia* sect. *GUILANDINA* also float and are dispersed by ocean currents.

Subfamily Caesalpinioideae is of some economic importance, although it is not nearly as important as subfam. Faboideae. The fleshy fruits of *Tamarindus indicus*, tamarind, and *Ceratonia siliqua* L., locust bean, carob, or St. John's bread, are minor food crops in some parts of the world. A gum used in paper-making and in food products is obtained from the seeds of *C. siliqua*. Several species of *Cassia* yield the drug senna, and species of *Cassia*, *Caesalpinia*, and various other genera are used in folk remedies. Several species of *Caesalpinia* are important sources of tannin. The wood of numerous species of Caesalpinioideae is hard, heavy, and beautifully grained. Genera with commercially important wood include *Brachystegia*, zebrawood; *Caesalpinia*, types of Brazil wood; *Cassia*; *Copaijera*, purpleheart; *Guibourtia* J. Benn., bubinga; *Haematoxylon* L., logwood; *Hymenaea*, courbaril; *Macrolobium* Schreber, zebrawood; *Mora* Benth; *Peltogyne* Vogel, purpleheart; *Peltophorum* (Vogel) Walp., canafistula; *Sindora*, supa; and *Swartzia*. Haematoxylin, used as a cytological stain and as a dye for wool, is obtained from the heartwood of *Haematoxylon campechianum* L.; brazil, a red dye, is extracted from the heartwood of several species of *Caesalpinia*; and sappan dye comes from *C. Sappan* L. Resins and copals are produced by species of *Copai-*

fera, *Cynometra* L., *Daniellia*, *Detarium*, *Gossweilerodendron* Harms, *Guibourtia*, and *Hymenaea*. Members of the Caesalpinioideae are often cultivated as ornamentals. Species of *Cercis*, *Gleditsia*, and, to a lesser degree, *Gymnocladus* are commonly seen in temperate regions, and species of *Amherstia* Wall.,³ pride of Burma, *Bauhinia*, orchid tree, *Brownea* Jacquin, mountain rose, *Caesalpinia*, *Cassia*, *Colvillea* Bojer ex Hooker, *Delonix*, *Parkinsonia*, *Peltophorum*, and numerous other genera are cultivated in tropical and subtropical areas.

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³ *Amherstia nobilis* Wall., sometimes called the most beautiful flowering tree in the world, rarely sets seed, is difficult to propagate from cuttings, and is sensitive to cool temperatures. Attempts to cultivate it in Florida have failed.

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KEY TO THE GENERA OF CAESALPINIOIDEAE IN THE
SOUTHEASTERN UNITED STATES

General characters: *trees or shrubs, rarely herbs; leaves mostly once pinnately compound, sometimes bipinnate, rarely appearing simple; rachises and leaflets with a basal pulvinus; stipels mostly absent; flowers mostly zygomorphic, papilionaceous only in Cercis; sepals imbricate; petals imbricate-ascending, with the upper petal innermost in bud; stamens 10 or fewer, mostly free; pollen grains shed singly; ovules anatropous; funiculus usually elongate; seeds without a U-shaped pleurogram (closed pleurograms present in some species of Cassia and a few other genera); hilum small, basal or subbasal.*

- A. Leaves compound; flowers \pm zygomorphic but not papilionaceous.
- B. Leaves primarily twice pinnately compound, the primary pinnae phyllodial in *Parkinsonia*.
- C. Leaves usually with several to many nonphyllodial pinnae and elongate petioles; leaflets small to large, not caducous; fruits various, usually not cylindrical-torulose; seeds arranged transversely.
- D. Flowers zygomorphic (bilaterally symmetrical), yellow to red, perfect (or if imperfect, the plants scramblers); calyx lobes completely inclosing petals in bud; shrubs, trees, or scrambling vines.
- E. Flowers small to moderately large, red and/or yellow; calyx lobes mostly imbricate in aestivation; fruits very variable, not strap-shaped with woody valves. 1. *Caesalpinia*.
- E. Flowers large, red to orange; calyx lobes \pm valvate in aestivation; fruits very long, strap-shaped, dehiscent, the valves woody. 2. *Delonix*.
- D. Flowers \pm actinomorphic (radially symmetrical), greenish, often imperfect; in bud petals visible between calyx lobes; deciduous trees.
- F. Trees lacking thorns; leaflets broadly ovate, entire; flowers long-pedicellate, in open racemes or small panicles; fruits dehiscent along the placental suture, the valves woody. 3. *Gymnocladus*.
- F. Trees armed with thorns; leaflets narrowly ovate with crenate margins; flowers short-pedicellate, in short racemes; fruits strongly flattened, indehiscent or tardily dehiscent, the valves chartaceous. 4. *Gleditsia*.
- C. Leaves usually with 2 elongate, flattened, phyllodial pinnae on a very short axis that ends in a spine; leaflets small, numerous along margins of pinnae, caducous; fruits cylindrical-torulose; seeds arranged longitudinally. 5. *Parkinsonia*.
- B. Leaves once pinnately compound, without phyllodial pinnae.
- G. Fertile stamens 4-10, filaments free; anthers usually basifixed, opening by terminal pores; petals \pm equal or 1 or 2 somewhat smaller than the others; fruits varied, but not brown and fleshy with a crustaceous outer layer. 6. *Cassia*.
- G. Fertile stamens 2, staminal and staminodial filaments connate for half their length into a sheath open on the adaxial side; anthers dorsifixed, dehiscing by longitudinal slits; petals very unequal, upper 3 large, lower 2 minute, scalelike; fruit large, brown, \pm sausage-shaped, fleshy, with a crustaceous outer layer. 7. *Tamarindus*.
- A. Leaves appearing simple, cordate; flowers papilionaceous. 8. *Cercis*.

Tribe CAESALPINIEAE Endl.

1. *Caesalpinia* Linnaeus, Sp. Pl. 1: 380. 1753; Gen. Pl. ed. 5. 178. 1754, "*Caesalpina*."

Shrubs, small trees, or scramblers, usually armed with recurved prickles. Leaves evenly [or oddly] twice pinnate, usually petiolate; rachises unarmed or with prickles; pinnae and leaflets several to many, opposite [or alternate], jointed basally; leaflets entire, eglandular [or with glands], the bases usually oblique; stipules absent or minute to conspicuously

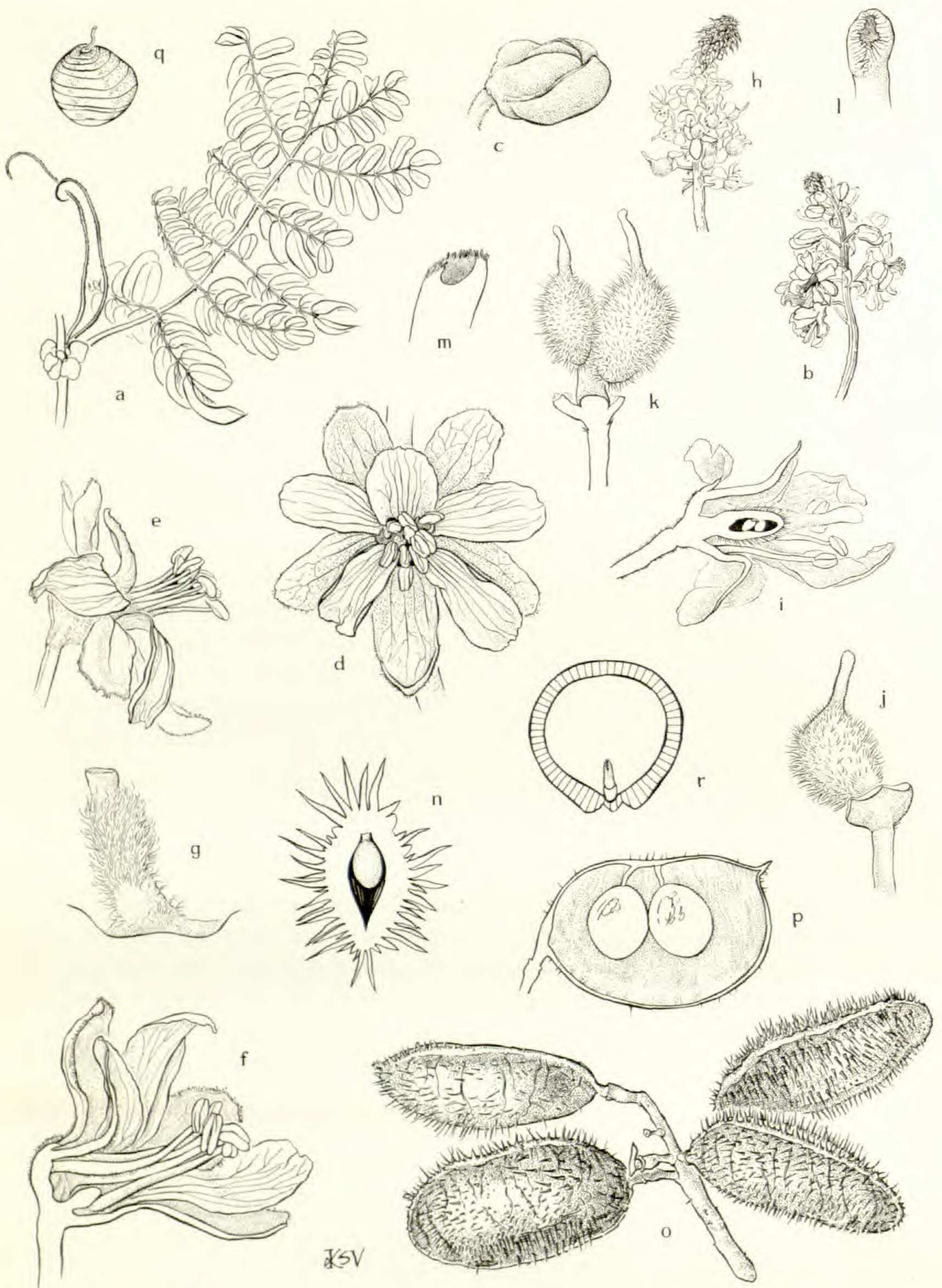


FIGURE 1. *Caesalpinia* section *Guilandina*. a-r, *C. Bonduc*: a, node with leaf, large persistent stipules, and axes of staminate inflorescences — note hooked prickles along rachis of leaf, $\times \frac{1}{4}$; b, tip of staminate inflorescence, the bracts persistent until anthesis, $\times \frac{1}{2}$; c, bud of staminate flower showing cucullate lower calyx lobe, $\times 2$; d, front view of staminate flower, $\times 2$; e, same in side view, $\times 2$; f, same in longitudinal section — note short floral cup and rudimentary gynoecium, $\times 3$; g, rudimentary gynoecium from staminate flower, $\times 12$; h, carpellate inflorescence, $\times \frac{1}{2}$; i, carpellate flower in longitudinal section showing the fertile carpel and well developed stamens lacking pollen,

leafy; stipels usually absent. Inflorescences several- to many-flowered, terminal or terminal and axillary [or falsely lateral] racemes or panicles, rarely reduced to solitary flowers; bracts usually caducous, sometimes persistent through anthesis; pedicels often jointed at base and near apex. Flowers perfect or imperfect in sect. *GUILANDINA*, the plants then dioecious. Calyx lobes 5, imbricate to almost valvate, nearly equal, the lower one sometimes cucullate and inclosing the others in bud, often same color as petals; calyx cup short [rarely campanulate]. Petals yellow and/or red, subequal and \pm sessile except for the keel petal with its tubular claw and small blade. Stamens 10, all fertile (in perfect and staminate flowers); filaments of 2 lengths, free, glandular-pubescent below; anthers dorsifixed, versatile, opening by longitudinal slits. Gynoecium free of calyx cup; ovary subsessile or shortly stipitate, glabrous, pubescent, glandular, or echinate; ovules 2-10; style elongate, usually equaling or exceeding anthers; stigmatic area usually in a small funnel-shaped depression at tip of style, sometimes fringed. Fruits very variable, usually flattened or compressed, wings absent [or present], dehiscent or not, with or without septae, the pericarp hard and woody or leathery to chartaceous, glabrous, glandular, or echinate. Endosperm usually absent. (Including *Guilandina* L. and *Poinciana* L.) LECTOTYPE SPECIES: *C. brasiliensis* L.; see I. Urban, Symb. Antill. 2: 280. 1900⁴; see also N. L. Britton & P. Wilson, Sci. Surv. Porto Rico Virgin Is. 5: 377. 1924. (Name in commemoration of Andrea Cesalpino, 1519-1603, Italian physician and botanical observer.)

A diverse group of the tropics and subtropics of both hemispheres and particularly abundant in drier areas of southwestern North America, Central America, and South America. Estimates of the number of species to be recognized if the genus is interpreted broadly range from 60 to 280 (Hattink says ca. 100). The genus is subdivided either into a series of sections (or subgenera), as was done by De Candolle and Bentham & Hooker, or into a number of segregate genera. Britton & Rose recognized 14 such genera in North America. Since the problem of generic delimitation can be solved only by critically examining the group on a worldwide basis, *Caesalpinia* is conservatively treated here in the inclusive sense. The genus has been studied mostly in regional floras and is badly in need of a major taxonomic review.

× 3; j, carpel shortly after anthesis, calyx lobes removed, × 2; k, gynoecium from aberrant flower with 2 carpels, × 2; l, front view of stigma showing trichomes surrounding stigmatic cavity, × 12; m, tip of style in section to show stigmatic cavity, × 12; n, cross section of ovary, one ovule visible, × 5; o, mature infructescence with indehiscent, echinate fruits, × ½; p, slightly oblique section of nearly mature fruit showing 2 seeds, × ½; q, mature seed with finely cracked seed coat, × ½; r, soaked seed in vertical section, seed coat hatched, × 1.

⁴ According to Urban (p. 286), three elements were included by Linnaeus in this species: Plumier's plant, which is the type of the genus; *Peltophorum brasiliense* (Sw.) Urban (= *Caesalpinia violacea* (Miller) Standley); and *Caesalpinia bahamensis* Lam.

Caesalpinia Bonduc (L.) Roxb. (*C. crista* of authors, not of Linnaeus, 1753, as typified by Dandy & Exell; *Guilandina Bonduc* L.; *G. bonducella* L., 1762; *C. bonducella* (L.) Fleming), gray nicker bean, is widespread, mostly as part of the coastal strand vegetation, in the tropics and subtropics of both the eastern and western hemispheres. In Florida, it occurs mostly along the coastal sand dunes and hammocks, at least from Palm Beach on the eastern shore southward to Key West, north along the western shore to St. Petersburg, and on offshore islands to Levy County. *Caesalpinia Bonduc* is distinguished by large leaflets with acute to acuminate apices, conspicuous, foliaceous stipules, an armature of stout prickles and thin, straight bristles, and warm-gray seeds. *Caesalpinia major* (Medicus) Dandy & Exell (*C. Bonduc* of authors, not of Linnaeus, 1753, as typified by Dandy & Exell), yellow nicker bean, with inconspicuous or no stipules, an armature of prickles only, and yellowish seeds, is also widespread in both hemispheres, but it is not as common as *C. Bonduc*. Small, Britton & Rose, and Long & Lakela attribute this species (as *C. Bonduc*) to southern Florida, but no specimens that can definitely be assigned to this species have been seen by the present authors. *Caesalpinia ovalifolia* Urban (leaflets small, elliptical to suborbicular, with rounded to emarginate apices; seeds spherical, yellowish) was also reported from southern Florida by Small and Britton & Rose, but again there seem to be no specimens from our area. This species belongs to a group largely restricted to the West Indies; the taxonomy of the complex is unsettled.

Caesalpinia Bonduc, *C. major*, and *C. ovalifolia* belong to sect. **GUILANDINA** (L.) Bentham & Hooker (*Caesalpinia* subg. *Guilandina* (L.) J. G. Baker in J. D. Hooker), a very distinct group of perhaps 18 or fewer species mostly of coastal strands in the New World. Species of sect. **GUILANDINA** are trailing or scrambling shrubs with the stems and leaf rachises armed with recurved prickles (rarely unarmed); the flowers are imperfect and the plants dioecious; the staminate inflorescences are bracteate during anthesis; the fruits are usually echinate (rarely smooth), elliptical or oval, laterally compressed, few-seeded, and nonseptate, with rigidly chartaceous valves that dehisce completely along the placental suture and apically along the abaxial suture; and the seeds are rather large, hard, globose to ovoid, slightly flattened or not, and usually colored gray, yellow, orange-brown, or black. The seeds float in seawater and may be transported long distances by ocean currents (see Gunn and Ridley).

Caesalpinia pauciflora (Griseb.) C. Wright, of sect. **CAESALPINIA**, occurs in pinelands on the northern part of Big Pine Key, Monroe County, Florida, that is underlaid by Miami oölitic limestone; it also occurs in Cuba and Hispaniola. This species is a small shrub (becoming a small tree in Cuba) with two prickles at each node; numerous small, ovate or elliptic leaflets; small, yellow, perfect flowers with petals and stamens that more or less equal the calyx lobes (the flowers evidently do not open very widely, at least in Florida); and small, smooth, flat, elongate,

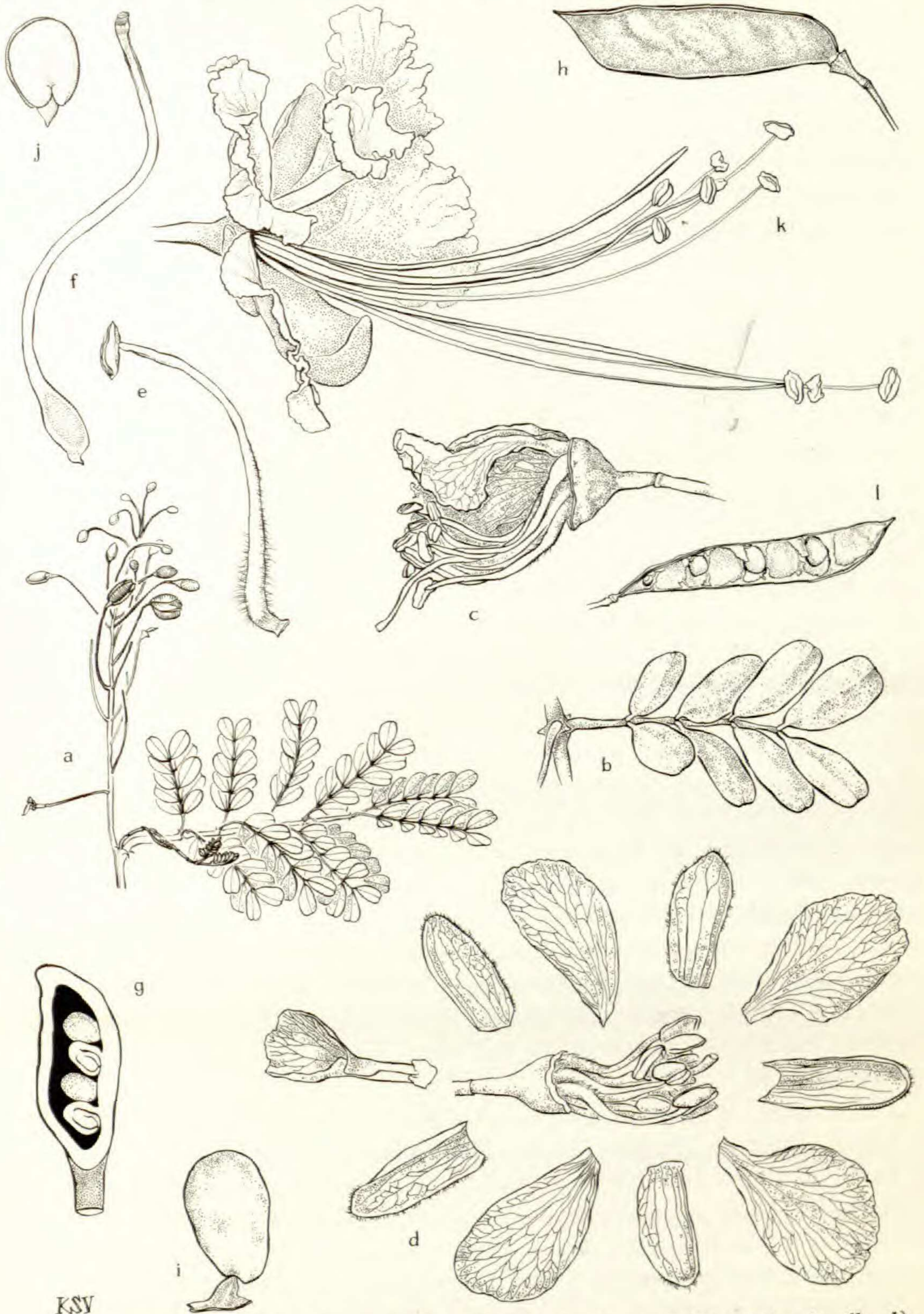


FIGURE 2. *Caesalpinia* sections *Caesalpinia* (a-j) and *Caesalpinaria* (k, l). a-j, *C. pauciflora*: a, tip of branch with bipinnately compound leaf and inflorescence, $\times \frac{1}{2}$; b, one pinna of leaf — note small spines at base, $\times 2$; c, side view of flower, calyx lobes and one wing and one keel petal removed, $\times 3$; d, “exploded” view of flower, $\times 3$; e, lower stamen, $\times 5$; f, gynoecium, $\times 5$; g, off-center vertical section of ovary showing parietal ovules in 2 rows, $\times 12$; h, fruit before dehiscence, $\times 1$; i, seed and funiculus, $\times 3$; j, embryo, $\times 3$. k, l, *C. pulcherrima*: k, flower — note clawed banner petal, $\times 2$; l, fruit, one valve removed, $\times \frac{1}{2}$.

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nonseptate fruits that dehisce completely along both sutures, the valves then becoming twisted.

The taxonomy of sect. CAESALPINIA is problematical, and it is not clear how many species belong to it. The type species of the genus, *Caesalpinia brasiliensis*, is a very poorly known species endemic to Haiti. Linnaeus's inclusion of three elements in this species (see footnote 4) has caused considerable confusion. Urban (p. 280) effectively lectotypified the species by the plate in Plumier. Plants related to *C. brasiliensis*, in addition to *C. pauciflora*, include about a dozen described species of the Greater Antilles and the Bahama Islands and *C. sessilifolia* S. Watson, of Durango and Coahuila, Mexico. *Caesalpinia brasiliensis* (as *C. Crista* L.) was included in sect. SAPPANIA DC. by De Candolle and by Taubert in Engler & Prantl.

Caesalpinia pulcherrima (L.) Sw. (*Poinciana pulcherrima* L.), pride of Barbados, of sect. CAESALPINARIA Bentham & Hooker, is a beautiful shrub or small tree that is widely cultivated and naturalized throughout the tropics and subtropics. In our area, it persists after cultivation and also reproduces from seed in southern Florida. Brenan suggests that this species is a native of tropical America; others attribute it originally to tropical Asia. The rather large flowers are in elongate terminal racemes (some also axillary). The pedicels are several times the length of the petals, and the stamens are greatly exserted. When the flowers first open, the keel and wing petals are red with yellow margins, and the small blade of the clawed banner petal is entirely yellow. Later, the yellow color disappears, and the flowers are then entirely red. The shade of red varies from bright red to scarlet or orange-red, and there are plants with flowers that are entirely and permanently yellow. The smooth, unarmed, laterally flattened fruits of *C. pulcherrima*, like those of sect. CAESALPINIA, dehisce completely along both sutures, with the valves then becoming twisted. One of the valves usually remains attached to the pedicel. There are several transversely arranged, obovate, compressed, dark brown seeds in each fruit; the seeds are separated from one another by well developed septae.

Other exotic species possibly naturalized in Florida include *Caesalpinia Gilliesii* (Wall. ex Hooker) Dietr., bird-of-paradise or paradise poinciana, a native of South America (see Vines); *C. Sappan* L., of India and Burma (*McFarlin* 4212 (A), Winter Haven, Polk County, Florida); and *C. Crista*, as typified by Dandy & Exell (*Ticanto Nuga* (L.) Medic.). A number of other species are grown as ornamentals in our area.

The bark of a number of species of *Caesalpinia*, particularly *C. coriaria* (Jacquin) Willd., divi-divi, *C. digyna* Rottl., *C. spinosa* (Mol.) O. Ktze., tara, and *C. melanocarpa* Griseb., are rich in tannins and are used both locally and commercially in the tanning of leather. Dyes are obtained from the fruit, bark, and wood of several species. Beautiful hardwoods that come from species of *Caesalpinia* include pernambuco wood (a type of Brazil wood) from *C. echinata* Lam.; sappan wood (another kind of Brazil wood) from *C. Sappan* L.; partridge wood from *C. Granadillo*

Pittier; and a type of ironwood from *C. ferrea* Mart. Decoctions of various plant parts from numerous species of *Caesalpinia* are used as herb remedies. The seeds of species of sect. *GUILANDINA* are made into jewelry. Several species, including *C. pulcherrima*, *C. Gilliesii*, and *C. decapetala* (Roth) Alston, are commonly cultivated in tropical and subtropical regions. The bark of *C. eriostachys* Benth and the stems and pulp of the fruits of *C. Crista* (*C. Nuga* L.) are used to stupefy fish.

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2. *Delonix* Rafinesque, Fl. Telluriana 2: 92. 1836.

Small to medium-sized unarmed trees with broad, rounded crowns and arching branches, the crown spread greater than height of tree, deciduous for brief periods or evergreen; twigs pubescent, with prominent lenticels; trunks buttressed at base; bark gray-brown, smooth, with many lenticels. Leaves alternate, evenly twice pinnate, with 10–25 pairs of pinnae, fairly large, the petiole with a basal pulvinus; pinnae opposite, with 12–40 pairs of leaflets and a basal pulvinus; leaflets opposite, quite small, finely pubescent on both surfaces, rounded at base and apex, nearly sessile, with a pulvinus; stipules simply or incompletely twice pinnate [or simple and subulate], caducous. Inflorescences elongate, several-flowered racemes at tips of growth of the season, overtopping the leaves; pedicels long, stout, articulated at each end; bracts ovate, with tapering apices, caducous. Flowers very showy, large, scarlet or red to orange, perfect, appearing with or before the leaves. Calyx lobes 5, green on abaxial surface, red with yellow border on adaxial surface, equal, thick, free, spreading, half as long as the petals, valvate in aestivation; calyx cup very short. Petals 5, long-clawed, becoming reflexed with age, wing and keel petals \pm equal, the banner petal larger. Androecium of 10 long-exserted stamens, all fertile; filaments slightly unequal in length, free to the base, curving adaxially, basally pubescent; anthers yellow and red, dorsifixed, versatile. Carpel shortly stipitate, inserted in center of small, nectiferous receptacle; ovary elongate, pubescent; style equaling or exceeding stamens, curving adaxially; stigma punctiform; ovules numerous. Fruits pendulous, septate, large (sometimes more than 0.6 m.), strap-shaped, straight or slightly scimitar-shaped, laterally compressed, woody, long-persistent, eventually opening along both sutures. Seeds numerous, sunken in transverse depressions in valves, narrowly [or broadly] ellipsoid, somewhat laterally flattened, red-brown, with lighter areas on each face; seed coat hard; embryo elongate, laterally flattened; endosperm present. Base chromosome number 24, 28. TYPE SPECIES: *Poinciana regia* Bojer ex W. J. Hooker = *D. regia* (Bojer ex W. J. Hooker) Raf. (Name derived from Greek *delos*, evident, and *onyx*, claw, in reference to the petals.)

A genus of three species, *Delonix regia* (a native of Madagascar, evidently rare in nature, widely cultivated throughout the tropics), *D. elata* (L.) Gambel (eastern Africa, southwestern Asia, India), and *D. Baccal* (Chiov.) Baker f. (eastern Africa). Capuron recently reduced *Aprevalia* Baillon to a section of *Delonix*, including in it seven species of Madagascar that had mostly been placed previously in *Aprevalia* or *Poinciana*.

Delonix regia, flamboyant, flamboyan, or royal poinciana, one of the most spectacular ornamental trees of the tropics, is commonly planted in southern Florida, and it is occasionally spontaneous in hammocks and pinelands. The trees are deciduous in areas where there is a distinct dry season, with the flowers appearing at the tips of the new growth of the

season on the seemingly bare trees. In our area, where rainfall is more uniform throughout the year, although the winters in Florida are dry, this species is mostly evergreen and the flowers overtop the leaves of the previous year. There are several color forms, with the overall color of the flower being scarlet, red, or orange. The calyx lobes are green on the abaxial surface and red (to orange, depending on the form) with yellow margins on the adaxial surface. The lateral and lower petals are red, with rather faint yellow streaks at the bases of the blades. The banner petal has red margins, with the central portion of the blade white with red streaks and the base of the claw bright yellow streaked with red. The banner petal evidently functions as a signal to pollinators, since it is fully expanded at anthesis, but the lateral margins soon roll inward and the white and yellow fade to red. This petal often falls from the flower before the wing and keel petals.

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3. *Gymnocladus* Lamarck, *Encycl. Méth. Bot.* 1: 733. 1785 ('1783').

Unarmed deciduous trees with narrow, rounded crowns; trunks forking into few, ascending main branches; branchlets stout, blunt, with a large pinkish pith; bark initially smooth, lenticellate, becoming very rough, with large plates attached along one side, and finally thick, with numerous, flat scales; axillary buds 2, superposed, in pubescent depressions; terminal bud absent; leaf scars large, irregularly cordate [or V-shaped], with 3-5[-13] rather indefinite bundle scars. Leaves large, mostly evenly bipinnate, long-petiolate, the petiole with a basal pulvinus; pin-

nae many-foliolate, the lower 1 or 2 pairs often reduced to single leaflets; leaflets shortly petiolulate, ovate to elliptical, with acuminate apices, entire margins, and slightly oblique bases; stipules lanceolate, caducous; stipels absent [or minute, awl-shaped, persistent]. Inflorescences erect [or drooping] racemes or panicles terminating growth of the year and from buds on wood of last year, those composed of carpellate flowers more elongate and racemose than those composed of staminate flowers; bracts and bracteoles small, caducous. Flowers regular, strongly fragrant, perfect or imperfect, the plants dioecious to occasionally polygamous. Calyx lobes 5, subequal, lanceolate, with acute apices, equaling and the same color as the petals, valvate in aestivation, but incompletely inclosing the petals; floral tube narrowly campanulate, 10-ribbed, pubescent and dark reddish purple without, lined with nectariferous tissue. Petals 5 (rarely 4), greenish white, sometimes dark reddish purple on the abaxial surface, pubescent, narrowly oblong with obtuse or acutish apices, keeled, imbricate in aestivation, inserted around opening of floral tube. Stamens 10, in 2 whorls of 5; filaments alternately long and short, free to the base, inserted as the petals; anthers dorsifixed, bright yellow or orange, polliniferous in staminate flowers, without pollen in carpellate flowers. Carpel well developed in carpellate flowers, variously reduced or rudimentary in staminate flowers, sessile or shortly stipitate, many-ovulate, inserted at base of floral tube; style short, stout, erect, exerted beyond anthers in carpellate flowers; stigma oblique, dilated, bilobed [or capitate]. Fruits pendent, obliquely stalked, laterally compressed, variously ovate, ellipsoid, oblong, or \pm falcate, 1-several-seeded, dehiscent along placental suture (but seeds retained in fruit), some persistent on trees through winter; valves dark reddish brown, glaucous or shiny, woody, smooth [or transversely ridged and grooved]; pulp surrounding seeds green, bitter, poisonous. Seeds large, compressed, broadly ovoid to obovoid or round, dark reddish brown, attached by a stout funiculus; seed coat thick, hard; embryo surrounded by a layer of cartilaginous endosperm. Germination hypogeal; juvenile leaves once pinnate. Base chromosome number 14. LECTOTYPE SPECIES: *G. canadensis* Lam. = *G. dioicus* (L.) Koch; typified by the removal of *G. arabica* Lam. to *Moringa* Adanson by Persoon, Syn. Pl. 1: 461. 1805; see also C. S. Sargent, Silva 3: 67. 1892. (Name derived from Greek *gymnos*, naked, and *klados*, a branch, alluding to the stout branches destitute of foliage for many months.⁵) — COFFEE-TREE.

A small genus of eastern North America and eastern Asia (the only genus of the Caesalpinioideae confined to these two regions), with *Gymnocladus dioicus* in eastern North America; *G. chinensis* Baillon in central

⁵ The name *Gymnocladus* has been treated as either masculine or feminine. According to Article 75A(2) of the 1972 edition of the *International Code of Botanical Nomenclature*, "generic names formed from two or more Greek or Latin words should take the gender of the last . . ." Since *klados*, transliterated into Latin as *cladus*, is masculine, it follows that *Gymnocladus* is also masculine.

and southeastern China; *G. assamicus* P. C. Kanjilal in Assam, India, and southeastern Yunnan, China; and *G. burmanicus* C. E. Parkinson in Lower Burma.

Gymnocladus dioicus, Kentucky coffee-tree, $2n = 28$, a tall tree with a few ascending branches and a narrow crown, stout twigs, and evenly bipinnate leaves that, considering their length, are among the largest of any tree in eastern North America, is native primarily to the west of the Appalachians from central New York to southeastern Ontario, Wisconsin, and southeastern South Dakota, southward to Kentucky, Tennessee, Arkansas, and Oklahoma; it is widely cultivated and has become naturalized to the north, south, and east of its original range. The species occurs mostly in low or rich woods as isolated trees or small colonies of widely separated individuals produced from root suckers sent up some distance from the parent tree; associated species include *Juglans nigra* (black walnut), *Acer saccharum* (sugar maple), *Tilia americana* (basswood), *Asimina triloba* (pawpaw), *Ulmus rubra* (slippery elm), *Fraxinus quadrangulata* (blue ash), *Populus deltoides* (cottonwood), and *Quercus rubra* and *Q. alba* (red and white oaks). Indians and early settlers sometimes planted *G. dioicus* near their dwellings, and the scattered distribution of the species is sometimes attributed to this practice. *Gymnocladus dioicus* is one of the last trees to expand its leaves in spring and the earliest to shed them in autumn, the leaflets turning yellow and falling from the rachis, which drops later.

The highly fragrant geraniol-scented flowers of *Gymnocladus dioicus* are moderately large, but they are greenish, not showy, and mostly radially symmetrical, with a long floral tube (containing abundant nectar). The petals and calyx lobes are about equal in length. The aestivation of the calyx is unusual in that it is incompletely valvate, with the lateral margins of the lobes not touching each other and the petals thus visible between them (FIGURE 3c). There are evidently two basic types of flower, each confined to different trees. Functionally staminate flowers, borne in compact panicles, have polliniferous anthers and a variously reduced but sterile gynoecium (FIGURE 3f, g). Morphologically perfect but mostly functionally carpellate flowers (the anthers lacking pollen) occur in elongate racemes or lax panicles (FIGURE 3b, h). Studies of the breeding system of *G. dioicus* in nature are lacking, but observations on several living trees cultivated in the Boston area and data from herbarium specimens indicate that this species is mostly dioecious, with some degree of polygamy. Two trees in the Arnold Arboretum that bear morphologically perfect flowers consistently set fruit, even though pollen appears to be lacking and there are no known staminate trees within a radius of several miles. The Asiatic species also appear to be predominantly dioecious.

The broad, elongate, somewhat compressed, reddish-brown fruits of *Gymnocladus dioicus* are retained on the tree after the leaves have fallen, with some remaining through winter. While the fruits are on the tree, or after they have fallen, the leathery-woody valves open slightly

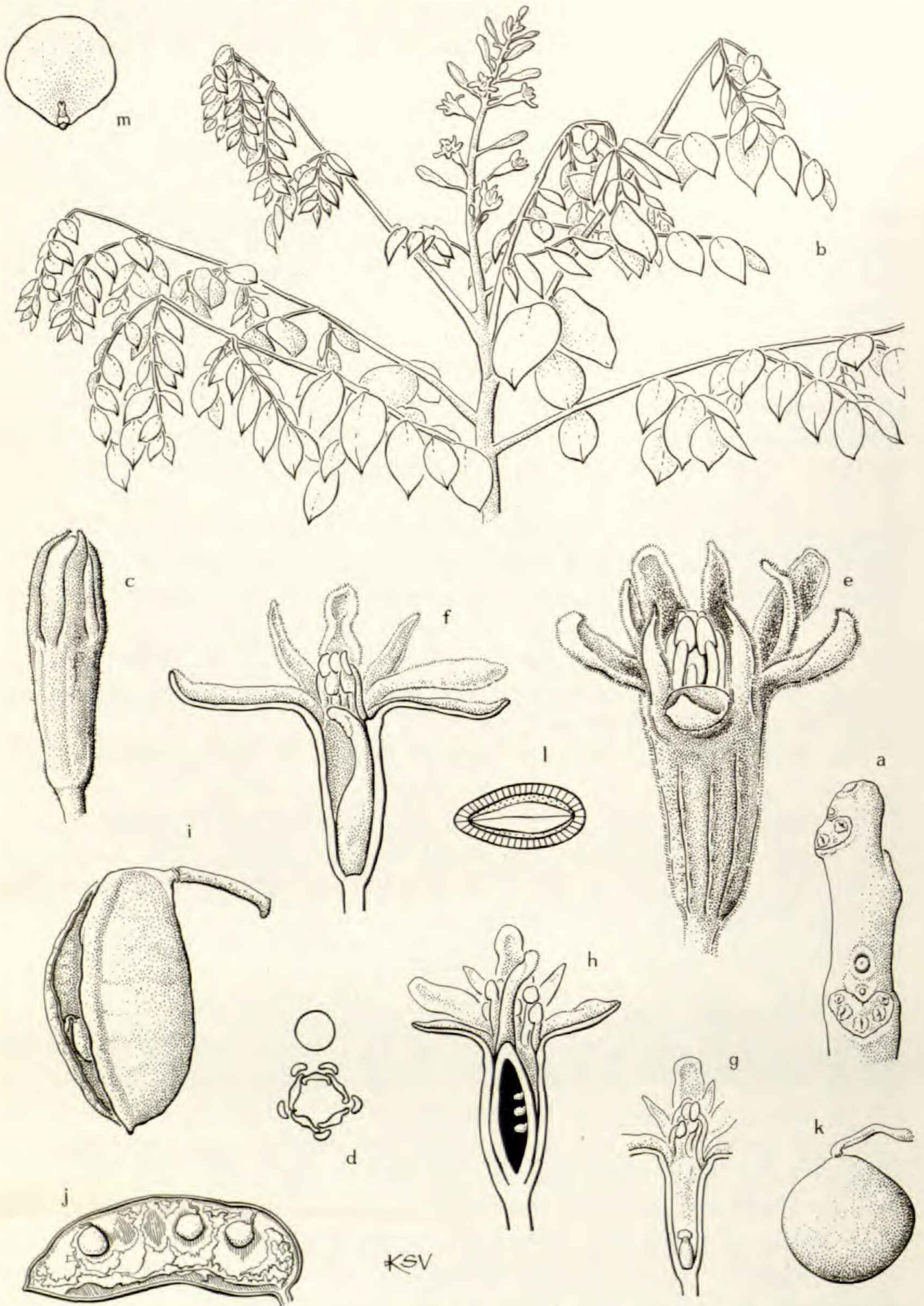


FIGURE 3. *Gymnocladus*. a-m, *G. dioicus*: a, winter twig, buds superposed, terminal bud absent, $\times 1$; b, tip of flowering branch, leaves bipinnately compound, $\times \frac{1}{4}$; c, flower bud, calyx lobes not completely covering petals, $\times 2$; d, diagrammatic cross section of flower bud to show aestivation, androecium and gynoecium not shown, inflorescence axis represented by circle — note that adaxial petal is innermost, $\times 2$; e, functionally staminate flower, $\times 3$; f, same in vertical section to show relationship of stamens and sterile gynoecium, $\times 2$;

along the placental suture, but the seeds are retained in the pod and are released only when the fruit is eaten by animals or when the valves decay. The seeds are surrounded by a green, sticky, bitter-tasting pulp. The large, compressed-globose seeds have a thick seed coat and may remain in the ground for many years before germinating.

About ten extinct species of *Gymnocladus*, mostly fossil leaf and fruit compressions, have been described from the central and western United States, Mexico, Europe, and China.

The fruits of *Gymnocladus* are rich in saponins, and those of *G. chinensis* and *G. assamicus* have been used for various washing purposes both in eastern China and among the Khasis in Assam, India. In a recent study of the chemical nature of the saponins and their sapogenins in *G. dioicus*, *G. chinensis*, and *G. assamicus* (Lee & Parkhurst, unpublished data), four major triterpenoid aglycones were found, with only minor quantitative differences between the species. The four compounds are different from, although structurally similar to, those found in species of *Gleditsia*. Saponin extracts from fruits of *G. chinensis* have blastocidal activity, and very low concentrations can terminate pregnancy in rats. This effect may be due to the cytotoxic action of the saponins on rapidly dividing embryonic cells (Parkhurst, pers. comm.).

The Pawnee and Meskwaki Indian tribes reportedly roasted the seeds of *Gymnocladus dioicus* like chestnuts for food, and early European settlers tried using the seeds as a coffee substitute. The wood of *G. dioicus* has been used locally for cabinet work and also for fence posts, since it is resistant to decay. This species is occasionally cultivated in parks and yards. People sometimes unwittingly plant this species, mistaking its seedlings for those of *Juglans nigra*, black walnut.

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g, portion of staminate flower with highly reduced gynoecium, $\times 2$; h, functionally carpellate flower in vertical section, anthers without pollen, $\times 2$; i, mature fruit dehiscing along adaxial (placental) suture, one seed visible, $\times \frac{1}{2}$; j, fruit, one valve removed, seeds surrounded by fleshy pulp (unshaded), $\times \frac{1}{4}$; k, seed with long funiculus, $\times 1$; l, cross section of seed, seed coat hatched, endosperm even-stippled, cotyledons unshaded, $\times 1$; m, embryo, one cotyledon removed, $\times 1$.

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4. *Gleditsia* Linnaeus, Sp. Pl. 2: 1056. 1753; Gen. Pl. ed. 5. 476. 1754.

Deciduous trees with open crowns [or shrubs]; trunks and branches usually armed with stout, simple or branched thorns; branches zigzagged, apically thickened; bark smooth, becoming lenticellate and eventually deeply fissured, with the ridges curved outward on one side; buds minute, several, superposed, the terminal bud absent; leaf scars irregularly U-shaped with 3 bundle traces. First leaves of the year (those preformed in buds of the previous year) evenly once pinnate, apparently fasciculate, the internodes short; later leaves evenly bipinnate with much longer internodes; leaflets small to medium-sized, numerous, subopposite to alternate, with crenate (rarely entire) margins and slightly oblique bases; stipules minute, caducous. Inflorescences axillary, solitary, or fascicled racemes [occasionally panicles] usually appearing with first leaves of the season; staminate inflorescences with numerous, congested flowers, the carpellate and perfect inflorescences lax, with fewer flowers; bracts scalelike, caducous. Flowers small, regular, perfect or imperfect, the plants polygamous to dioecious. Calyx lobes 3–5, subequal, colored like and as large as the petals, deciduous, valvate in aestivation, but incompletely inclosing petals; floral tube campanulate, lined with nectariferous tissue. Petals as many as the calyx lobes, subequal, not clawed, greenish to creamy white, inserted at margin of floral tube, imbricate in aestivation. Staminate flowers with 4–6[–10] exserted stamens; filaments filiform, free to base, pubescent below, inserted at apex of floral tube; anthers subequal, dorsifixed; gynoecium rudimentary or absent. Carpellate flowers with 4–6[–10] staminodia, the anthers small to aborted, lacking pollen; gynoecium sessile or very shortly stipitate, inserted at base of floral tube; style short, oblique; stigma prominent, dilated, bilobed, \pm perpendicular to axis of flowers; ovules 2–many. Perfect flowers similar to carpellate ones, except some anthers polliniferous. Fruit stipitate, strongly flattened laterally [or merely compressed], broadly elliptical and one-seeded or elongate, many-seeded, and variously straight, falcate, undulate, or twisted; pericarp chartaceous [to woody], smooth or conspicuously veined, sometimes glaucous, indehiscent or tardily dehiscent; pulp present or absent. Seeds transverse in fruit, separated by membranaceous septae or not, broadly ellipsoid to subquadrate, compressed; seed coat light brown to greenish brown, thin; embryo surrounded by thick layer of cartilaginous endosperm. Germination epigeal, juvenile

leaves once pinnate. Base chromosome number 14. TYPE SPECIES: *G. triacanthos* L. (Name commemorating J. G. Gleditsch, 1714–1786, German botanist; spelling sometimes erroneously altered to *Gleditschia* or *Gleditzia*.) — HONEY LOCUST.

A small genus of about 14 species disjunct in four regions: two or three species in eastern North America; *Gleditsia amorphoides* (Griseb.) Taub. in northern Argentina and adjacent Uruguay, Paraguay, and Brazil; *G. caspica* Desf. in the area surrounding the Caspian Sea; *G. assamica* Bor, a very poorly known species from northeastern India; and eight species in Asia from eastern, central, and southwestern China to Korea, Japan, Vietnam, and the Philippine Islands. *G. africana* Benth (Senegal to the Sudan Republic, south to Zambia, Rhodesia, and Southwest Africa) is now considered to be a species of *Erythrophleum* R. Br. (see Brenan, 1967, subfamily references).

Gleditsia triacanthos, honey locust, $2n = 28$, characterized by the indehiscent, elongate, many-seeded fruits with the seeds surrounded by a sweet pulp and separated by membranaceous septae, is a common tree of the midwestern United States, where it occurs in a variety of habitats, from moist woods along rivers and streams to dry or upland slopes and pastures. The natural distribution of this species is from western New York and extreme southwestern Ontario (introduced?) to southeastern South Dakota southward to eastern Texas and along the western edge of the Appalachian Mountains to northwestern Florida. *G. triacanthos* is widely cultivated and has become naturalized east of the Appalachians from South Carolina to New England and Nova Scotia and perhaps also to the west of its original range. *Gleditsia aquatica* Marsh. (*G. monosperma* Walt.), water locust, $2n = 28$, is largely ecologically and geographically isolated from *G. triacanthos*, occurring in swamps and low wet woods and along the borders of bayous and sloughs on the Coastal Plain from eastern South Carolina to central Florida and eastern Texas and northward in the Mississippi and Ohio River valleys to Missouri, Kentucky, Illinois, and Indiana. The fruits of *G. aquatica* are mostly one-seeded, short, tapering-elliptical in outline, strongly flattened, light in weight, without pulp, and tardily dehiscent.

Plants with fruits intermediate between those of *Gleditsia triacanthos* and *G. aquatica* were first discovered in Brazoria County, Texas, by Sargent, who named them *G. texana*; he later suggested that these intermediate forms might be of hybrid origin. Similar plants have since been found in scattered areas in Indiana, Arkansas, Mississippi, and Louisiana (evidently always in the area where the distributions of *G. triacanthos* and *G. aquatica* overlap). The taxonomic disposition of these plants differs, some authors placing them within the range of variation of *G. triacanthos* (see illustration on p. 533 of Vines, subfamily references, for variations that occur in Brazoria County, Texas), others recognizing them as a distinct species, *G. texana*, and still others considering them to be F_1 hybrids, *G. × texana* Sargent (pro. sp.).

Simple to complexly branched thorns, generally considered to be modified lateral branches, are found on the twigs, branches, and/or trunks of all species of *Gleditsia*. The abundance and size of the thorns vary greatly, both on the same individual and between individuals of the same species. In *G. triacanthos* the thorns decrease in frequency toward the

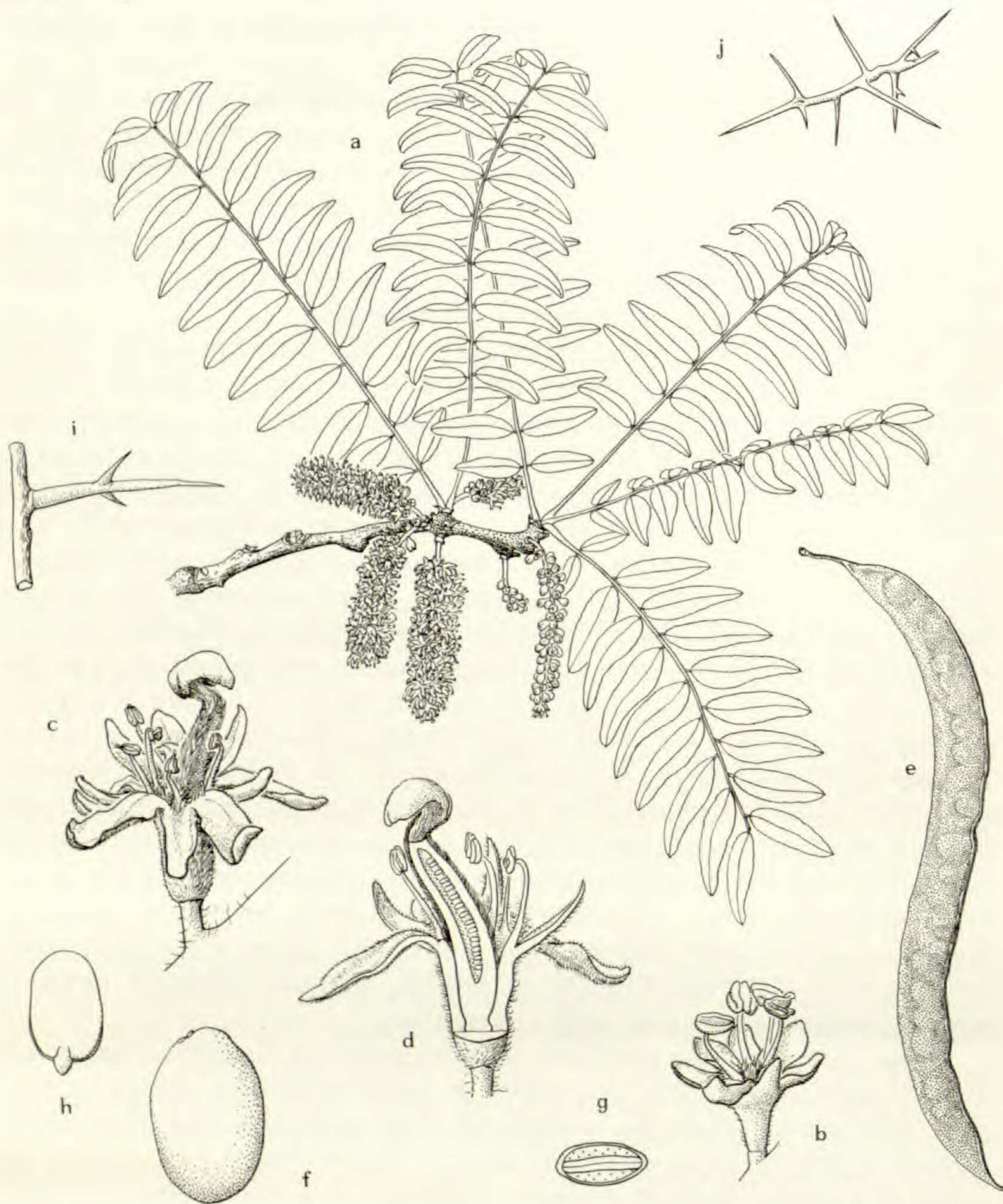


FIGURE 4. *Gleditsia*. a-j, *G. triacanthos*: a, tip of branch with staminate inflorescences — note once pinnately compound leaves on short shoots, $\times \frac{1}{2}$; b, staminate flower with 4 stamens, $\times 3$; c, carpellate flower, $\times 3$; d, same in vertical section — note perigynous insertion of calyx lobes, petals, and stamens and orientation of gynoecium, $\times 4$; e, mature fruit, $\times \frac{1}{4}$; f, seed, $\times 2$; g, soaked seed in cross section, endosperm even-stippled, seed coat and cotyledons unshaded, $\times 1$; h, embryo from soaked seed, $\times 1$; i, thorn from branch, $\times \frac{1}{4}$; j, thorn from tree trunk, $\times \frac{1}{4}$.

top of the trees, and "thornless" trees may be produced by grafting buds taken from near the top of a tree onto normal rootstocks. Included in *G. triacanthos* f. *inermis* (L.) Zabel are the various "thornless" cultivars, but none of these plants are totally devoid of thorns.

Very little is known about the root systems of the species of *Gleditsia*. *Gleditsia triacanthos* produces a strong taproot and a profusely branched lateral root system that penetrates the soil to a depth of 10 to 20 feet. The root system of *G. aquatica* is apparently adapted to swampy conditions. No root nodules have been reported in *Gleditsia*.

The flowers are usually imperfect, but they are sometimes perfect. In *Gleditsia triacanthos* individual trees evidently may have only staminate flowers, carpellate/perfect flowers, or all three types of flowers. Branches of a tree tend to have only one type of flower. Since herbarium specimens are usually prepared from a single branch, only extensive field studies can ascertain the degree of polygamy or dioecism in this species. However, the situation in *G. triacanthos* and other species in the genus may be considered as an intermediate step toward complete dioecism.

The fruits of *Gleditsia* vary considerably from species to species. Two groups may be recognized, species with fruits that contain pulp and those in which it is lacking. Some of the pulp-containing fruits are woody and subcylindrical; others are chartaceous and strongly laterally compressed. The very light fruits of *G. aquatica* are probably dispersed primarily by wind and water. The fruits of *G. triacanthos* are larger and heavier, but they are still capable of being carried by wind and water. Moreover, the fruits and/or seeds of *G. triacanthos* are readily eaten by cattle, squirrels, rabbits, and rats, with some of the seeds passing intact through the animals' digestive tracts.

The fruits of *Gleditsia* are rich in saponins, and the pods of *G. sinensis* Lam., *G. japonica* Miq., and *G. fera* (Lour.) Merr. are used as soap substitutes in China, Japan, and Indochina. Preliminary analyses indicate that eight major triterpenoid sapogenins or aglycones are found in *G. triacanthos*, *G. sinensis*, and *G. officinalis* Hemsley, with oleanolic acid and echinocystic acid (identification tentative) being the predominant compounds (Parkhurst & Lee, unpublished data). Although final separation and identification of these compounds are pending, it is clear that all three species have the same set of sapogenins. It is noteworthy that *Gleditsia* evidently shares no major sapogenins with *Gymnocladus*.

A chromosome number of $2n = 28$ has been reported in *Gleditsia amorphoides*, *G. aquatica*, *G. fera* (southern China and Vietnam), *G. microphylla* Gordon ex Y. T. Lee⁶ (central China), *G. japonica* (as *G. horrida* Willd., northeastern China, Korea, and Japan), *G. ? sinensis*, and *G. triacanthos*. Recent studies on Asiatic species of *Gleditsia* by Y. T. Lee indicate that both *G. sinensis* (eastern and central China) and *G. australis*

⁶ *Gleditsia microphylla* Gordon ex Y. T. Lee, nom. nov. *G. heterophylla* Bunge, Mém. Acad. Sci. St. Pétersbourg Savants Étr. 2: 29. 1833, not *G. heterophylla* Raf., Fl. Ludovic. 99. 1817. TYPE: China, in mountains near Lun-Zuan-ssy and Ssi-jui-ssy, A. Bunge s.n., 1831 (K!).

Hemsley (southern China and Vietnam) share the same diploid number as the others.

Some 40 extinct *Gleditsia* or *Gleditsia*-like species have been reported in the literature. These fossils are mostly compressions of leaflets, thorns, fruits, or silicified wood; no microfossils have been found. Fossils of *Gleditsia* have been found in places outside the present range of the genus (e.g., Europe and western North America), indicating a much wider distribution of the genus in the past.

Gleditsia triacanthos is widely cultivated as an ornamental in the United States, especially in those areas where *Ulmus americana* has been seriously affected by the elm disease (*Ceratocystis ulmi*). It is also commonly cultivated in Europe and Asia (for names of cultivars see Wagenknecht, 1961).

The pulp around the seeds of *Gleditsia triacanthos* is sweet, and the pods are used as a trail food and an ingredient in folk beers. Wild animals and cattle readily eat the pods. The thorns on the trunks and branches of this species have been used as sewing needles, as tools for carding wool, and, when tied to sticks, as weapons by country people for hunting bullfrogs (Steyermark, Fl. Missouri, p. 873). The wood of *G. triacanthos* is very strong and durable and has been used for fence posts and railroad ties. The Cherokee Indians of Tennessee reportedly made bows from the wood of this plant. The wood of *G. aquatica* is also strong and durable. It is used for fence posts and has qualities that would make it a fine cabinet wood.

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5. *Parkinsonia* Linnaeus, Sp. Pl. 1: 375. 1753; Gen. Pl. ed. 5. 177. 1754.

Armed evergreen shrubs or small trees, branching near base, with broad, very open crowns; branches slender, often pendent, slightly zigzagged; bark thin, yellow-green, smooth, eventually becoming reddish brown and breaking into small flakes or plates; buds solitary or superposed. Leaves alternate, evenly twice pinnately compound, with 2, infrequently 4 or 6, opposite pinnae on a very short main axis that terminates in a spine (the whole leaf appearing as 2 or more simply pinnate leaves); rachis of pinnae elongate, flattened, narrow, persistent, and phyllodial; leaflets opposite to partly alternate, sessile, numerous, small, deciduous; stipules spinescent, persistent or caducous; axillary leaves lacking spines, sometimes produced in fascicles from axils of primary leaves. Inflorescences solitary or fascicled, slender, elongate, several-flowered racemes axillary on growth of the year, appearing with the leaves; pedicels slender, about as long as the diameter of the flowers, jointed just below them, subtended by a small, scalelike, caducous bract. Flowers perfect, moderate-sized, showy, fragrant. Calyx synsepalous, the lobes 5, equal, narrowly triangular, reflexed at anthesis, strongly imbricate in bud, deciduous; calyx cup shorter than lobes, obliquely campanulate, persistent. Petals 5, much longer than the calyx lobes, nearly equal, bright yellow fading to reddish, spreading, shortly clawed, slightly erose, the banner petal with conspicuous red spots and a longer, basally glandular claw. Androecium of 10 stamens in 2 series of 5, shorter than the petals; filaments free to the base, the one opposite banner petal enlarged at base, gibbous on abaxial side; anthers dorsifixed, versatile. Gynoecium shortly stipitate, pubescent when young; style slender, curving adaxially, equaling or slightly exceeding stamens; stigma minute; ovules numerous. Fruits pendent, cylindrical, constricted externally between and beyond the seeds (torulose), tapering at both ends, the wall rather thin, longitudinally striate, the exocarp separating in strips from the endocarp, supposedly tardily dehiscent by 2 valves. Seeds few, widely spaced, longitudinally arranged, oblong, slightly flattened, smooth, brown; seed coat thin; endosperm abundant on either side of embryo; embryo bright yellow, the cotyledons flattened, broadly ellipsoid, auriculate at base, the radicle short, broad, straight. Base chromosome number 7. TYPE SPECIES: *P. aculeata* L. (Name commemorating John Parkinson, 1567–1650, English florist, apothecary, herbalist, and author.) — JERUSALEM-THORN.

One or more species of southwestern North America and perhaps also of Central and South America and Africa. The generic limits have been variously interpreted. Watson (1876) considered the differences between

Parkinsonia and *Cercidium* Tulasne (nine taxa currently recognized by Carter; Texas, Sonoran Desert to Peru and Argentina), to be insignificant and merged the two under *Parkinsonia*. Sargent reestablished *Cercidium* and recognized two American species of *Parkinsonia* (*P. aculeata* and *P. microphylla* Torrey) and one species from southwestern Africa (*P. africana* Sonder). The two genera were redefined by Johnston, who considered *Parkinsonia* to include only *P. aculeata* and *P. africana* and *Cercidium* to be composed of nine species (including *C. microphyllum* (Torrey) Rose & Johnston, which was later segregated by Britton & Rose as the monotypic genus *Cercidiopsis*). While reviewing some African members of the Caesalpinioideae, Brenan concluded that *Peltophoropsis scioana* Chiov., of East Africa, along with a new species also from East Africa, and the American species of *Cercidium* (including *Cercidiopsis*) were best included within *Parkinsonia*. Carter (1974a) pointed out that a satisfactory resolution of the generic relationships in this group of plants can only be reached after they have been studied biologically, morphologically, cytologically, and genetically. She added, however, that "*Cercidium* forms a discrete . . . unit confined to the Americas" and that "study of Brenan's comparative chart . . . shows that among the taxa included, *Parkinsonia aculeata* is the most discordant element." Carter suggested, furthermore, that "*Parkinsonia* be considered a monotypic genus comprised of *P. aculeata* Linnaeus" and that "the relationships of the three African species (*P. africana*, *P. anacantha*, and *P. scioana*) be considered further before accepting them as congeneric with *Parkinsonia* and *Cercidium* as proposed by Brenan." Because of the varying concepts of *Parkinsonia*, the description given in the present treatment refers only to *P. aculeata*.

Parkinsonia aculeata, Jerusalem thorn, horsebean, retama, Mexican palo verde, $2n = 14$, is probably indigenous to Texas, New Mexico, Arizona, and Mexico. It is widely cultivated in warm climates throughout the world, particularly in arid regions, and is prone to escape and become naturalized. In our area, it is known at least from Beaufort County, South Carolina, to Key West, Florida, and north and west to southern Georgia and Louisiana.

Putative natural hybrids between *Parkinsonia* and *Cercidium* have been reported by Carter & Rem from Sonora and Guerrero, Mexico (*P. aculeata* \times *C. praecox*) and Texas (*P. aculeata* \times either *C. texanum* or *C. macrum*).

One of the most striking features of *Parkinsonia aculeata* is the foliage. The leaves are evenly bipinnate, with one to three (rarely to six) pairs of opposite pinnae on a short petiole and rachis. The axes of the pinnae are strongly flattened, narrow, and quite long and drooping, giving the plants a graceful appearance. Numerous, tiny leaflets are borne alternately or oppositely along the edges of the pinnae; these fall during periods of drought, the axes of the pinnae evidently functioning as the principal photosynthetic organ of the plant. The rachises of the pri-

mary leaves (those leaves produced along the current year's growth of a long shoot) are modified into stout, unbranched spines that persist on the branches after the pinnae are shed. On some plants the stipules that subtend primary leaves also are spinescent. Spine-tipped rachises and stipules are not usually found on the secondary leaves (those produced in fascicles on short shoots in the axils of primary leaves), and no other types of spine are found in this species. Carter (1974) pointed out that the primary leaves and spines of *P. aculeata* are different from those of *P. africana* and species of *Cercidium*.

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Tribe CASSIEAE Bronn

6. *Cassia* Linnaeus, Sp. Pl. 1: 376. 1753; Gen. Pl. ed. 5. 176. 1754.

Shrubs, [trees,] or annual or perennial herbs [rarely scrambling or climbing], unarmed [very rarely with prickles or thorns]. Leaves evenly pinnate [rarely absent and the branches then photosynthetic]; petioles with an adaxial groove; leaflets 2 to many, small to large, sometimes sensitive to touch, symmetrical or basally oblique, with a median, eccentric, or marginal midrib [or several parallel veins]; conspicuous sessile or stipitate, variously shaped glands often present on petiole and/or rachis; stipules bristlelike, subulate, linear, falcate, or leafy, persistent or caducous. Inflorescences axillary or terminal, few- to many-flowered, lax or condensed racemes or terminal panicles or the flowers solitary; bracts various, usually of 2 sets, one at base of floral axis, another subopposite pair below each flower. Flowers perfect, rarely imperfect and the plants then polygamous, sometimes enantiostylous, small to large and showy, usually only slightly bilaterally symmetrical (except for the androecium). Calyx lobes 5, \pm equal [to strongly unequal], imbricate in aestivation; calyx cup short to nearly absent. Petals 5 [rarely 1 or 2], nearly rotate, \pm equal or some smaller, scarcely clawed, yellow (sometimes drying white or pinkish) or less commonly pink, red, or white, sometimes with basal nectar guides, conspicuously veined or not, imbricate. Stamens 10 [rarely reduced to 4 or 5], all fertile or some reduced to staminodes, the fertile ones \pm equal or strongly unequal; filaments long to short or nearly absent, \pm equal or strongly unequal, glabrous, free, terete [or with swollen areas]; anthers basifixed or infrequently dorsifixed, dehiscent by terminal pores or slits, rarely by basal pores or longitudinal slits, uniform or the abaxial [or adaxial] ones larger, sometimes curved, often constricted above with variously shaped apices. Ovary sessile or stipitate, elongate, often curved, free of the calyx cup, with several to many ovules; style short or elongate, usually curved; stigma terminal, small or rarely ciliate or swollen. Fruits very variable, cylindrical to flat, [rarely winged], indehiscent or dehiscent (sometimes elastically so) and opening along one or both sutures or irregularly dehiscent, woody to coriaceous or membranaceous, with or without septae, sometimes containing pulp. Seeds mostly transverse, sometimes oblique or longitudinal, large to small, flattened or not, ovoid to elongate, rhomboid, rectangular, or trapezoidal; seed coat occasionally smooth, otherwise with fine lines, longitudinally arranged or scattered pits, or closed pleurograms; funiculus long or short. Endosperm present. Embryo spathulate, with flattened or irregularly folded cotyledons. Base chromosome numbers 7 and 8. (Including *Adipera* Raf., *Chamaecrista* Moench, *Chamaesenna* Raf., *Ditremexa* Raf., *Emelista* Raf., *Peiranisia* Raf., and *Psilorhegma* Britton & Rose.) LECTOTYPE SPECIES: *C. fistula* L.⁷; see N. L. Britton & A. Brown, *Illus. Fl.*

⁷This species has been removed to the segregate genera *Cathartocarpus* Persoon and *Bactrylobium* Willd. but is accepted generally as the lectotypic species of *Cassia*

No. U. S. Canada ed. 2. 2: 335. 1913; see also A. S. Hitchcock & M. L. Greene, Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 152. 1929. (The Greek name of some (lauraceous?) aromatic plant; Theophrastus applied this name to the plant now known as *C. acutifolia* L.)

One of the largest genera of Leguminosae. Bentham (1871) recognized 338 species in his study, the latest worldwide revision, and Irwin (1964) estimated that there have been about 350 species described since that time. The genus is most diverse in the tropics and subtropics, particularly in the Americas. Some species of sections ONCOLOBIUM, PROSOSPERMA, and CHAMAECRISTA extend into the temperate regions of South and/or North America. *Cassia* is very diverse morphologically, and Britton & Rose, following the precedent of Rafinesque, recognized 28 segregate genera as native or introduced to North America. Such fragmentation has not been accepted generally. The subgeneric classification scheme outlined by Bentham, which has been shown to be a quite natural arrangement and is still widely followed, is used here. Bentham's often quoted statement about *Cassia* is worth repeating: "To botanists it presents an excellent instance of a large, widely distributed, much varied, but well-defined group. So natural, indeed, is the genus that, notwithstanding the great contrast in habit between the splendid arborescent *Fistulas* and some of the weedy herbaceous *Prosospermas*, or *Chamaecristas*, and although its principal characters are derived from the pod and the anthers, which both present more diversity than in any other Leguminous genus, yet there is hardly a species which has ever, by any tolerably fair botanist, been falsely or carelessly included or rejected from the genus, except perhaps in the case of a few garden seedlings which had not yet flowered."

Bentham subdivided *Cassia* into three subgenera, eight sections, two subsections, and 30 series. In the southeastern United States, species representing two subgenera and four sections occur indigenously, and another two sections are represented by naturalized species. In addition, a number of exotic species are cultivated in southern Florida; some of these persist from cultivation and may eventually become naturalized.

Subgenus SENNA Bentham (shrubs, trees, or herbs; foliar glands present or absent; leaflets usually rather large; sepals obtuse; androecium variable but usually with one abaxial and three adaxial staminodes, four short fertile adaxial stamens, and two elongate fertile abaxial stamens; anthers basifixed, the tips often constricted and elaborate, dehiscing by apical pores or chinks; fruits variable, dehiscent or not, often with a longitudinal septum, rarely with pulp; seeds usually with a distinct pleurogram on each face, rarely smooth) is represented in our area by nine species in five sections.

Four of these species belong to sect. ONCOLOBIUM Vogel ex Bentham (leaflets several to numerous; glands one per leaf, inserted toward base

L. Incidentally, *C. fistula* is the twelfth species of *Cassia* enumerated by Linnaeus in the *Species Plantarum*.

of petiole; fruits subcylindric to compressed; seeds transverse or oblique). The closely related *Cassia marilandica* L. (*C. Medsgeri* Shafer) and *C. hebecarpa* Fernald (*Ditremexa marilandica* sensu Britton & Rose; *C. marilandica* of authors, not L.), both commonly known as wild senna, are perennial herbs with 10–20 elliptical to slightly ovate, apically mucronate leaflets per leaf and blackish, elongate, strongly flattened fruits. *Cassia marilandica* can be distinguished from *C. hebecarpa* by the short-appressed, rather than densely long-villous, indument of the ovaries; by the glabrate or short-hirtellous fruits with segments much shorter than broad, rather than loosely villous fruits with segments as long as broad; and by the plump, obovoid, rather than flattened, quadrate seeds. *Cassia marilandica* is widespread in our area, occurring from Pennsylvania to Iowa, south to Florida and Texas. *Cassia hebecarpa* is more northeastern in its distribution, ranging from New England to Wisconsin, southward to North Carolina, eastern Tennessee, northern Georgia, and Alabama.

Cassia occidentalis L. (*Ditremexa occidentalis* (L.) Britton & Rose), coffee senna, $2n = 28$, a tall annual herb with 6–12 tapering-ovate leaflets per leaf, globose petiolar glands, and elongated, compressed fruits with thickened sutures, is a native of tropical Central and South America that has become naturalized from Florida to Texas, north to Virginia, Indiana, Illinois, Iowa, and Kansas; it is also introduced in the tropics of the Old World. *Cassia ligustrina* L. (*Ditremexa ligustrina* (L.) Britton & Rose), a small shrub with 12–16 narrowly ovate or lanceolate, basally oblique leaflets per leaf and conic-cylindrical petiolar glands, occurs mostly in hammocks in central and southern Florida and also on the Greater Antilles, Bermuda, and Grand Cayman Island.

Cassia obtusifolia L. (*C. Tora* of authors, not L.; *Emelista Tora* sensu Britton & Rose), sickle-pod or coffee-weed, of sect. PROSOSPERMA Benthams (leaflets 2 to numerous, rather large; petiolar gland(s) situated between the lowest pairs of leaves; fruits subterete, 4-angled, or compressed-lomentaceous; seeds longitudinal) is a pantropical weed that extends northward in eastern North America from Florida and Texas to Pennsylvania, Indiana, Michigan, Illinois, Missouri, and Kansas. According to Brenan (subfamily references), this species has generally been confused with *C. Tora* L., a species confined to Asia. *Cassia obtusifolia* can be separated from the other species of *Cassia* in our area by its annual duration; broad, obovate leaflets with a cylindrical gland situated between the lowest pair; few-flowered, seemingly axillary inflorescences; linear, curved fruits; and rhomboid seeds. The embryo of *C. obtusifolia*, unlike that of most other species of the genus, has folded cotyledons.

Section CHAMAESENNA DC. (leaf glands situated between the lower pair or pairs of leaflets or absent; leaflets moderate-sized to large; fruits usually compressed or flattened; seeds flattened) is represented in our area by *Cassia bahamensis* Miller (*Peiranisia bahamensis* (Miller) Britton & Rose). This species is a shrub with basally oblique, ovate, elliptic, or obovate, mostly mucronate leaflets that have small glands scattered on the lower surfaces and along the midrib on the upper surfaces and with large,

globose glands on the leaf rachises between the lower pairs of leaflets. It occurs mostly in pinelands in southernmost Florida in the vicinity of Miami, the Everglades, and on some of the southwestern Florida Keys (No Name Key, Big Pine Key, Key West); it also occurs on Cuba and some of the Bahama Islands. Several species of sect. *CHAMAESENNA* are commonly cultivated in southern Florida, including *C. alata* L. (*Herpetica alata* (L.) Raf.), a native of tropical America, and *C. didymobotrya*

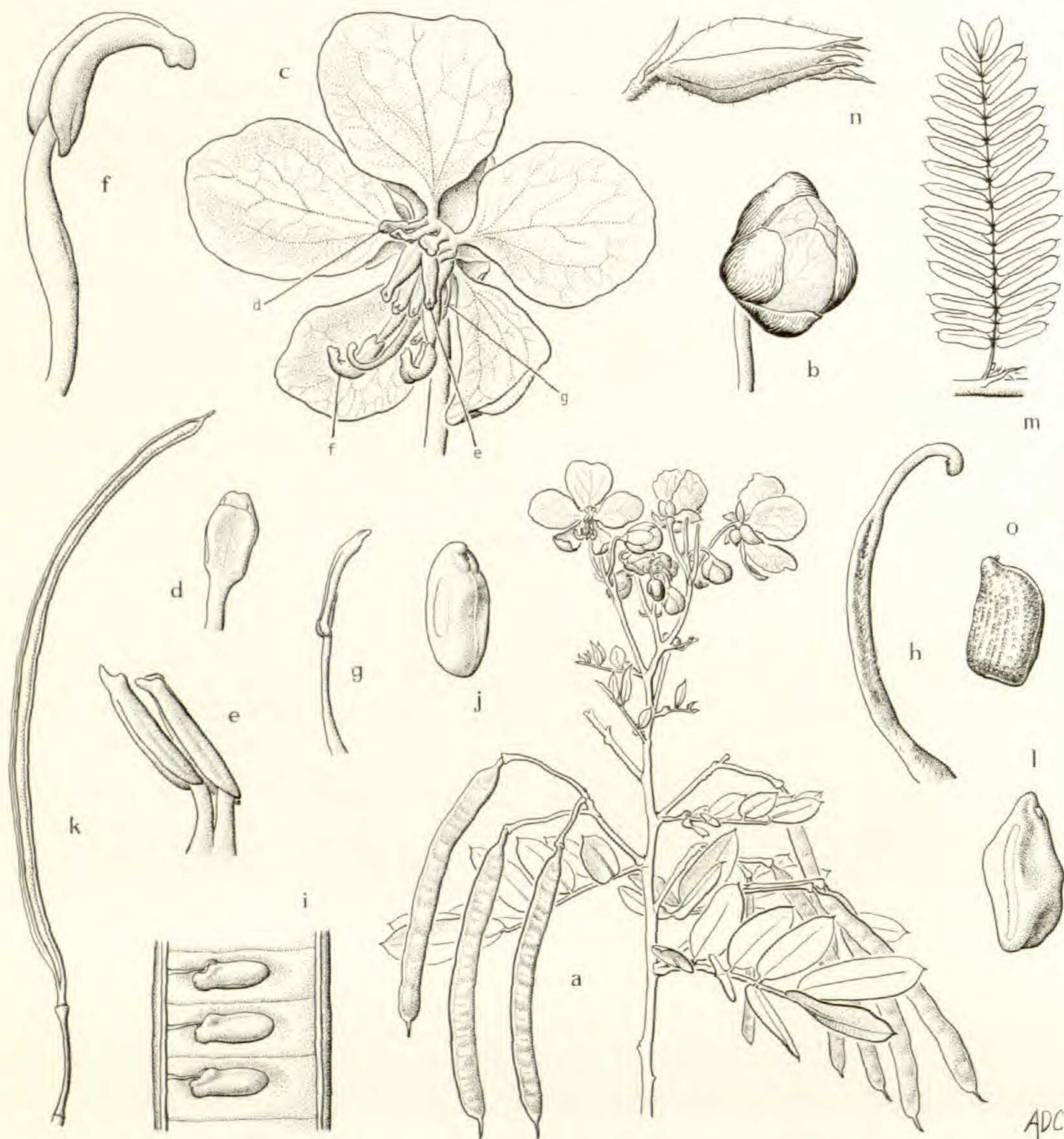


FIGURE 5. *Cassia*. a-j, *C. bahamensis*: a, flowering branch with immature fruits, $\times \frac{1}{2}$; b, front view of opening flower bud to show sepals and aestivation of petals, $\times 2$; c, flower, $\times 2$; d, upper staminode (1 of 3), $\times 4$; e, functional lateral stamens (2 of 4) opening by terminal pores, $\times 4$; f, functional lower stamen (1 of 2), $\times 4$; g, lower staminode, $\times 4$; h, gynoeceum, $\times 4$; i, portion of immature fruit opened to show developing seeds with threadlike funiculi, $\times 3$; j, oblique view of seed — note lateral, closed pleurogram, $\times 4$. k, l, *C. obtusifolia*: k, fruit, $\times \frac{1}{2}$; l, seed — note narrow, closed pleurogram, $\times 4$. m-o, *C. fasciculata* var. *fasciculata*: m, pinnately compound leaf with persistent stipules, $\times \frac{1}{2}$; n, bud to show tapering-acute sepals, $\times 2$; o, seed marked with numerous small pits arranged in rows, $\times 4$.

Fresenius (*Chamaesenna didymobotrya* Small), of tropical Africa; Small noted the occurrence of the latter species in vacant lots in Miami, Florida.

Cassia surattensis Burman f. (*C. glauca* Lam., *C. suffruticosa* König, *Psilorhegma suffruticosa* (König) Britton), of sect. PSILORHEGMA Benth (stamens 10, all fertile; filaments short; fruits flattened), is a native of tropical Asia widely cultivated in tropical regions and occasionally naturalized in hammocks in southern Florida.

Cassia bicapsularis L. (*Adipera bicapsularis* (L.) Britton & Rose) of sect. CHAMAEFISTULA DC. (mostly shrubs; foliar glands situated between the lower pairs of leaflets or absent; fruits terete, turgid, dehiscent along the adaxial suture or not; seeds transverse, separated by transverse septae) occurs along canal and road banks and in marshes in southern Florida, as well as in the West Indies, Mexico, and Central and South America. This species is distinctive in its relatively large, obovate leaflets, globose foliar glands, large yellow flowers, two abaxial stamens with greatly elongated filaments, and mostly straight, cylindrical fruits with ovoid, slightly flattened, smooth or faintly pitted seeds. *Cassia corymbosa* Lam. (*Adipera corymbosa* (Lam.) Small) a native of Argentina and Uruguay, has fruits and seeds similar to those of the preceding species, but it has slightly smaller flowers, narrowly ovate leaflets, and cylindrical foliar glands. According to Small, this species is occasionally adventive along the Coastal Plain from Georgia to Louisiana and Tennessee.

The largest number of species of *Cassia* in the southeastern United States belong to sect. CHAMAECRISTA DC. of subg. LASIORHEGMA Benth (fruits elastically dehiscent; funiculus short; seeds with numerous pits usually arranged in rows). Benth divided sect. CHAMAECRISTA into two subsections, subsect. XEROCALYX, which Irwin has elevated to the rank of section, and subsect. LEIOCALYX; all of the southeastern species belong to the latter and are annual or perennial, sometimes suffrutescent herbs with small, mostly numerous leaflets, persistent stipules, several-flowered axillary racemes, membranaceous, pointed calyx lobes, and an androecium of unequal stamens with polliniferous anthers. In their treatment of the Caesalpinoid legumes for the *North American Flora*, Britton & Rose (following Greene) recognized the genus *Chamaecrista* Moench with 111 species, subdividing them into 17 groups of undesignated rank. Five of their groups occur in our area. *Cassia rotundifolia* Persoon (*Chamaecrista rotundifolia* (Persoon) Greene), the only species of group Rotundifoliae, is a prostrate perennial with leaves having only two leaflets and lacking petiolar glands. It has been reported from near Orlando, Florida, as well as from Mexico, Central and South America, the West Indies, and western Africa. *Cassia serpens* L. (*Chamaecrista serpens* (L.) Greene), of group Pilosae, has been reported from Florida by Ward. This species is a tap-rooted, woody-based herb with cylindrical petiolar glands and strongly unequal petals; it occurs primarily in the West Indies and Central and South America. *Cassia keyensis* (Pennell) MacBride (*Chamaecrista keyensis* Pennell), of group Lineatae, is a soft-hirsute, suffrutescent perennial with many branches from a contorted rootstock and large yellow flowers. It

has been considered endemic to Big Pine Key, No Name Key, and Key West, Florida, but Ward has recently included it within *C. grammica* Sprengel, a West Indian species.

The remaining species of sect. CHAMAECRISTA in the southeastern United States belong to group Fasciculatae, which has been treated quite variously in floras (cf. Small, Britton & Rose, Fernald, Gleason, Radford *et al.*, and Long & Lakela) and in recent reviews and lists (Turner, Pullen, Ward). Two species complexes can be recognized. The first, with very short pedicels, stalked petiolar glands, and small flowers with five stamens and short anthers, includes *Cassia aspera* Muhl. ex Ell. (petiolar gland cylindrical, "odd petal" only slightly longer than the others), which occurs in pine-lands and sandy areas from southeastern South Carolina along the coast of Georgia to the Florida Keys, and *C. nictitans* L. (*Chamaecrista multipinnata* Pollard, *Ch. procumbens* (L.) Greene), wild sensitive plant (head of petiolar gland globose, "odd petal" nearly twice as long as the others), which is found in acid, sandy or rocky soils of open woods, upland slopes, ridges, bluffs, prairies, fallow fields, and open thickets from Florida to Texas, north to Massachusetts, Vermont, New York, Ohio, Indiana, Illinois, Missouri, Kansas, and Oklahoma. The latter is especially variable in pubescence, and several varieties have been proposed.

The second complex of group Fasciculatae includes species that have longer pedicels, mostly sessile petiolar glands, larger flowers, and ten elongated anthers. Eight species of this complex of "partridge peas" were recognized in North America by Britton & Rose, with six in our area. These are *Chamaecrista brachiata* Pollard, *Ch. fasciculata* (Michx.) Greene, *Ch. robusta* Pollard, *Ch. depressa* (Pollard) Greene, *Ch. mississippiensis* Pollard, and *Ch. littoralis* Pollard. *Chamaecrista Deeringiana* Small & Pennell was included by Britton & Rose with some perennial species of southwestern North America in their group Deeringianae, but this species is now considered to be a member of the *Cassia fasciculata* complex. Recent authors have interpreted this complex as a single polymorphic species, and they have either considered it meaningless to attempt to account in a taxonomic system for the variation that occurs in this group, or they have recognized a number of varieties that admittedly intergrade with one another. This complex as it occurs in the United States was most recently reviewed by Pullen (unpublished Ph.D. thesis), who considered *C. Deeringiana* (Small & Pennell) MacBride (scattered from central Georgia to southern Florida and southwestern Alabama) to be distinct from *C. fasciculata* Michx., which he subdivided into eight varieties. According to Pullen, five of these varieties occur in our area: *C. fasciculata* var. *fasciculata* (Florida to Texas, north to Massachusetts, New York, Ontario, Ohio, Indiana, Wisconsin, Minnesota, and South Dakota), var. *littoralis* (Pollard) MacBride (North Carolina, Georgia, northern Florida, Alabama, Mississippi, Louisiana, and Texas), var. *robusta* (Pollard) MacBride (mostly sympatric with var. *fasciculata*, but not extending into peninsular Florida), and var. *Tracyi* (Pollard) MacBride (Georgia, northwestern Florida, Alabama, Mississippi, Arkansas, Louisiana, and Texas; apparently disjunct

in Illinois). The name of the fifth variety (ranging from Delaware to southern Florida) is based on *Cassia brachiata* Pollard, but Pullen's combination is still unpublished.

Several species of subg. CASSIA (subg. FISTULA Bentham), including *Cassia fistula* L., golden shower, *C. grandis* L. f., pink shower, *C. nodosa* Hamilt., *C. javanica* L., and *C. renigera* Wall. ex Bentham, are cultivated in southern Florida. Members of this subgenus are trees with leaves lacking foliar glands; the sepals are obtuse; the ten stamens are all fertile, but the three abaxial ones are at least twice as long as the seven adaxial ones; the anthers are not basifixed, and they open (within the same flower) by incomplete longitudinal slits and by basal pores; the fruits are indehiscent and often contain pulp; and the seeds are smooth, transversely arranged in the fruits, and separated by complete septae.

The flowers of many species of *Cassia* show enantiostyly (the occurrence of left- and right-handed flowers), with the flowers differing in the direction in which the style is bent and in the relative position of the different calyx lobes and petals. This phenomenon is particularly evident in the *Cassia fasciculata* complex, where the larger "odd" petal (which is not the banner petal) occurs on the side of the flower that is away from the stem.

The androecium of *Cassia* is remarkably diverse in the fertility, size, shape, mode of dehiscence, and, to a lesser degree, number of stamens. In subg. CASSIA (subg. *Fistula* Bentham) there are ten stamens in two whorls, all with fertile anthers. Stamens of the outer whorl are of two types — the three abaxial ones have very elongate, S-curved, sometimes nodose filaments and large anthers, while the two adaxial ones have short, straight filaments and small anthers. All anthers of the inner whorl dehisce by two incomplete subapical and two incomplete subbasal slits. The five stamens of the inner whorl are of intermediate size and have basally 2-spurred anthers that dehisce by subbasal pores located at the tips of the spurs. The androecium of members of subg. LASIORHEGMA consists of ten, or infrequently five, stamens that are all fertile and alike in form, structure, and dehiscence, although they differ somewhat in size within a flower. The filaments are rather short and the anthers are basifixed, apically bilobed, and dehiscent by apical chinks. The anthers of subg. LASIORHEGMA are unique in that the lateral sutures are prevented from opening by rows of closely coiled and interlocked trichomes. Subgenus SENNA is more variable in androecial structure, and some species may have ten stamens that are all fertile and more or less alike. However, in most species of this subgenus in our area, three adaxial stamens are reduced to small, spathulate staminodes; four lateral stamens are fertile and have filaments and anthers of varying lengths; and three abaxial stamens have greatly elongated, curving filaments and large, polliniferous anthers. In some species the central abaxial stamen is smaller than the others and may lack pollen. The fertile anthers in subg. SENNA dehisce by terminal pores or chinks and are tipped by modified, often elaborate structures that presumably have some function

in pollination. For a detailed review of the androecium of *Cassia*, see the series of papers by Venkatesh.

Little is known about plant-insect relationships involving *Cassia*, but in view of the diversity of the flowers, particularly of the androecium, and the frequent presence of extrafloral nectaries (the foliar glands), it would seem that this is a good area for future investigations. The few reports of pollination indicate that there are several different systems. Stevens reports that in *C. marilandica* bees land on the carpel and three lower stamens and then bite open the four middle anthers, removing the pollen to their pollen baskets. Charles Robertson, however, observed that on this species, and on *C. Chamaecrista*, bees stroke the anthers with their mandibles, thus "milking" the pollen out of the terminal pore. In any case, the two long stamens on either side of the style furnish pollen for pollination. A case of "buzz" pollination is reported by Buchmann in *C. Quiedondilla*. In this case bees land on the flower and curl their bodies tightly over the long pollinating anthers; they then vibrate their indirect flight muscles, causing a small cloud of pollen to come out of the terminal pores.

The seeds of *Cassia* are also of taxonomic value. In subg. CASSIA they are smooth, shiny, and sometimes marked with faint to distinct cracks in the outer seed coat. These cracks may be more or less uniform on the seed or more prominent on the faces. Occasionally, seeds may have a few faint, minute pits, and in some species there is a line running from the hilum across one or both faces to the top of the seed. Apparently the majority of species of subg. SENNA have seeds with a distinct raised or depressed and/or differently colored area called a pleurogram (areole, *lineafisural*, face area) on each side. The shape and size of the pleurogram varies considerably from species to species, but it is always closed and thus differs from the U-shaped pleurograms found in most species of Mimosoideae. The seeds of *C. bicapsularis* and *C. corymbosa*, of subg. SENNA, lack pleurograms and greatly resemble seeds typical of subg. CASSIA; these and related species should be examined more closely. The seeds of plants of subg. LASIORHEGMA seem always to be marked with numerous, usually prominent pits that may be arranged in longitudinal rows or randomly scattered over the surface. For a summary of the internal morphology of seeds of *Cassia*, see Okpon. Polyembryony and facultative apomixis have been observed in several species of the largely Australian sect. PSILORHEGMA of subg. SENNA. Janzen has made a detailed study of the predation of *C. grandis* seeds by bruchid beetle larvae.

Chromosome numbers are known for about 100 species representing all subgenera and sections of *Cassia*. The genus is rather complex cytologically, with several base numbers, polyploidy, and aneuploidy. Within subg. CASSIA, sporophytic numbers of 24 and 28 have been reported. Subgenus SENNA is diverse, with the following sporophytic numbers reported for each section: sect. CHAMAEFISTULA, 24, 26, 28, 52 (with 28 the most frequent count); sect. ONCOLOBIUM, 24, 26, 28, 56 (with 28 again predominant and some of the early counts of 24 and 26 questionable); sect. PROSOSPERMA, 22, 26, 28 (the uniglandular form of *C. obtusi-*

folia of the southeastern United States and the West Indies is $2n = 28$, while the biglandular form of northern South America is $2n = 26$); sect. CHAMAESENNA, 16, 24, 28; and sect. PSILORHEGMA, 14, 28, 42, 56 (see Randell for an analysis of this largely Australian group). Section ABSUS of subg. LASIORHEGMA appears to be uniformly $2n = 28$. The two subsections of sect. CHAMAECRISTA consistently differ in base chromosome number, with $x = 7$ and $2n = 14$ in subsect. XEROCALYX and $x = 8$ and $2n = 16$ or rarely 32 or 48 in subsect. LEIOCALYX. Irwin & Turner suggest that the base chromosome number in *Cassia* is 7, with the derived numbers 13, 12, and 11 arising by aneuploid loss from various euploid levels. The base number of 8 in subsect. LEIOCALYX presumably would have arisen by the aneuploid gain of one chromosome.

The drug senna, used as a cathartic, comes from the dried leaves of *Cassia Senna* L., Alexandrian senna, and *C. angustifolia* Vahl, Tinnevelly senna (nomenclature that of Fairbairn & Shrestha). The leaves or fruits of a number of other species, including *C. fistula*, *C. grandis* L. f., *C. javanica* L., *C. marilandica*, *C. moschata* H.B.K., and *C. Sophera* L., are used locally for the same purpose. Infusions of the leaves of *C. alata*, *C. absus* L., *C. sericea* Sw., *C. Sophera*, *C. obtusifolia*, and *C. Tora* L. are used in treating skin diseases, particularly ringworm. *Cassia laevigata* Willd., *C. obtusifolia*, *C. occidentalis*, and *C. sericea* have been used locally as coffee substitutes. A mordant used in combination with blue dyes is obtained from the seeds of *C. Tora*. The roots of *C. nodosa* Lam. are used locally as a soap substitute. The wood of several species, including *C. javanica*, *C. nodosa*, *C. siamea* Lam., *C. Sieberiana* DC., and *C. timoriensis* DC., is hard, heavy, and often beautifully grained and is used locally. The pods of *C. grandis* are high in pectin, and a gum similar to guar (obtained from *Cyamopsis tetragonoloba*) can be obtained from the seeds of *C. occidentalis*; both of these species have been suggested as potential commercial crops. A number of species, including *C. alata*, candelabra bush, *C. bicapsularis*, Christmas bush, *C. fistula*, golden shower, *C. grandis*, pinkshower cassia, *C. javanica* (including *C. nodosa* Roxb.), pink cassia, *C. siamea*, *C. spectabilis* DC., yellow shower, and *C. surattensis*, are commonly cultivated in tropical and subtropical regions, including southern Florida. The rainbow shower tree, commonly seen in Honolulu, is a hybrid between *C. fistula* and *C. javanica*.

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Tribe AMHERSTIEAE Bentham emend. J. Léonard

7. *Tamarindus* Linnaeus, Sp. Pl. 1: 34. 1753; Gen. Pl. ed. 5. 20. 1754.

Medium to large, unarmed, evergreen trees with short, thick trunks, rounded crowns, and widely spreading branches; twigs zigzagged, pubescent when young; bark rough, fissured; buds solitary, sessile, the terminal one absent. Leaves alternate, evenly once pinnate, shortly petiolate, the petiole with a basal pulvinus; leaflets opposite, small, numerous, the apices rounded and shortly mucronate, folding against the rachis at night, translucent dots absent, the margins \pm parallel, the bases asymmetrically rounded, nearly sessile, with a wrinkled basal pulvinus; stipules free, asymmetrical, caducous. Inflorescences terminal or axillary, pendulous, several-flowered, rather lax racemes shorter than the leaves; bracteoles 2, well developed, bright pink, inclosing young flower buds, valvate, caducous. Flowers perfect, moderate-sized; buds red. Calyx lobes 4, equal, reflexed at anthesis, white to pale yellow on adaxial surface, reddish on abaxial surface, more than twice as long as the turbinate floral tube, imbricate in aestivation. Petals unequal, the upper 3 elliptic to obovate, yellow-gold with red veins, recurving widely, slightly exceeding the calyx lobes, the lower 2 minute, scalelike. Fertile stamens 3, exerted above the petals, their filaments curving adaxially, monadelphous for half their

length into a sheath open on the adaxial side, with teeth representing staminodia alternating with free portions of filaments; anthers dorsifixed, versatile, opening by longitudinal slits. Carpel long-stipitate, the gynophore adnate to the floral tube; style elongate, stout, curving adaxially, swollen apically, and topped by a tuft of stigmatic papillae. Fruit pendent, indehiscent, sausage-shaped with irregular constrictions, somewhat compressed laterally, reticulate, brown at maturity, with a dry, thin outer layer, a pulpy middle layer including several fibrous strands, and a coriaceous inner layer forming septae between the seeds, the outer layer cracking into irregular plates as the fruits dry. Seeds 1-10 per fruit, rhomboid, laterally compressed, shiny chestnut brown, with a continuously margined pleurogram on each face; seed coat hard, the outer layer becoming mucilaginous when wet; embryo large; endosperm absent. Base chromosome number 12. TYPE SPECIES: *T. indica* L. (Name from Arabic *tamr*, date, and Latin *indus*, Indian.) — TAMARIND.

A single species, *Tamarindus indica*, tamarind, widely cultivated in tropical areas. Its native range is impossible to determine at present, but it is indigenous to the savannas of Africa and was probably introduced into India at an early date. Additional species described from northeastern tropical Africa are best included with *T. indica*, according to Brenan. The tamarind is cultivated in southern Florida as a shade tree and for its fruits. It has evidently become naturalized in Lee County and on some of the Florida Keys.

The inflorescences of *Tamarindus indica* are pendulous, but the flowers are not resupinate. Consequently, the flowers are in a morphologically upside-down position. At anthesis the floral tube bends abaxially (i.e., upward, in relation to the ground), so that the axis of the flower is more or less perpendicular to the ground. In this position the androecial sheath and the carpel arch obliquely upward over the three large petals, the inner surfaces of which form a horizontal landing place for pollinators. As an insect lands on the petals and crawls toward the opening of the nectariferous floral tube, any pollen on the insect's back is transferred to the stigma and a new load is acquired from the three fertile anthers.

The tamarind is a most useful plant. The trees are evergreen and very ornamental; large specimens are resistant to strong winds and light frost. The wood, hard, heavy, and fine-grained, is used locally for tools and cabinet work and makes an excellent charcoal (formerly used in gunpowder). However, *Tamarindus* is usually grown as a fruit tree. The pulp of the ripe fruits has high concentrations of both sugar and tartaric acid; it is eaten fresh or extracted and used in making fruit drinks, curries, chutneys, candy, ice cream, sauces, sweetmeats, preserves, jellies, medicinal preparations, and brines for pickling fish. The pulp is one of the major ingredients in Worcestershire sauce. Overripe fruits may be used to remove tarnish from copper and brass. The seeds are edible and can be made into flour. Sizing for cloth, paper, and jute products is made from the seeds, as well as vegetable gum and oil. The leaves and

green twigs are used as flavoring agents, and the leaves and flowers are eaten in salads. The leaves yield a yellow dye.

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Tribe CERCIDEAE Bronn, "Cerceae"

8. *Cercis* Linnaeus, *Sp. Pl.* 1: 374. 1753; *Gen. Pl.* ed. 5. 176. 1754.

Deciduous, rather flat-topped, unarmed, small to medium-sized trees or shrubs with zigzagged branches; bark with small, loose scales; axillary buds paired, superposed, the upper ones shortly stalked, the lower ones sessile and covered by top of leaf scar, the bud scales shortly fringed; vegetative buds 2-scaled, at nodes toward tip of growth of previous season, flowering buds several-scaled, at nodes toward base of growth of previous season and on older growth; terminal bud lacking, the growth consequently sympodial; leaf scars raised, decurrently ridged from the nodes, round-triangular, fringed at the top, with 3 bundle traces. Leaves appearing simple (evidently derived from fusion of 2 leaflets), alternate, 2-ranked, long-petiolate, the largest at tips of branches; blades with cordate bases, entire margins, and tapering-acute [obtuse or emarginate] apices, with 5, 7, or 9 prominent palmately arranged veins; petioles swollen at each end; stipules small, scalelike, caducous, leaving no scar. Inflorescences sessile umbel-like clusters [or elongate racemes] along growth

of the previous and earlier years and on the trunk, flowering before and as the leaves expand; pedicels jointed, colored like the calyx; bracts small, scalelike, often imbricate at base of inflorescences. Flowers perfect, 5-merous, papilionaceous in appearance. Sepals connate into a bilaterally symmetrical, basally enlarged, magenta, persistent floral cup; calyx lobes 5, short, triangular. Petals 5, free, clawed, purplish pink or rarely white, inserted on the floral cup, the upper, adaxial, banner petal smallest and inclosed in bud by the 2 lateral wing petals and 2 keel petals. Androecium of 10 free stamens, inclosed by the keel petals; filaments thickened, pubescent below, persistent, inserted on the floral cup, the alternate ones shorter; anthers versatile, all fertile, 2-locular at maturity, opening by longitudinal slits. Ovary shortly stalked, inserted obliquely at base of floral cup; style tapering, curved upward; stigma terminal, knoblike; ovules numerous. Fruit stalked, laterally flattened, tapering at each end, narrowly winged on the adaxial side, prominently veined, reddish, shiny, often tardily dehiscent along both sutures, the margins parallel or the abaxial one curved inward at each end. Seeds usually 3-6 on slender funicles, orbicular to oblong, compressed; seed coat crustaceous, bright red-brown; embryo surrounded by a thin layer of endosperm; cotyledons flattened, orbicular to oblong; radicle superior. Base chromosome number 14. TYPE SPECIES: *C. Siliquastrum* L.; see C. S. Sargent, *Silva N. Am.* 3: 93. 1892. (Name from Greek *kerkis*, weaver's shuttle, perhaps alluding to the shape of the fruit; Theophrastus used this name for a leguminous plant, evidently *C. Siliquastrum*.) — REDBUD, JUDAS TREE.

About eight species in four widely separated areas: *Cercis canadensis* L. in eastern North America southward to northeastern Mexico; *C. occidentalis* Torrey ex Gray in western North America; *C. Siliquastrum* in southern and eastern Europe (probably indigenous only from Turkey eastward to Afghanistan); and five species described from China. The Chinese species are *C. chinensis* Bunge (widely distributed in temperate China, most abundant in western Hupeh and eastern Szechwan), *C. racemosa* Oliver (eastern Szechwan and adjacent Hupeh), *C. Chuniana* Metcalf (Kwangsi), *C. Chingii* Chun (Anhui and northern Kwangtung), and *C. pauciflora* Li (Szechwan). The taxa of eastern North America and eastern Asia are morphologically similar to one another, as are those of western North America and Europe.

Cercis canadensis, redbud or (in parts of our area) Judas tree, ranges from southern Connecticut and New York south to central Florida and west to Michigan, southern Wisconsin, Iowa, eastern Nebraska and Kansas, much of Oklahoma and Texas (except for the panhandles), and northeastern Mexico (Tamaulipas, Coahuila, Nuevo León, San Luis Potosí, Hidalgo). The only report of the species outside of cultivation in Canada is that of a tree that formerly grew on Pelee Island in Lake Erie, Essex County, Ontario. Throughout most of the range of the species, the mature leaves are thin, dull green on both surfaces (young leaves are

glossy and reddish) and have tapering-acute apices; these plants, var. *canadensis*, occur from the northern and eastern limits of the species southwestward to eastern Texas (see Turner and Correll & Johnston, Man. Vasc. Pl. Texas). The young leaves are usually pubescent below, with some trichomes remaining on the mature leaves. Individuals with glabrous leaves are f. *glabrifolia* Fernald. Southwestward from the Arbuckle Mountains of Oklahoma, some or all populations have leaves that are rather coriaceous, rich deep green, shiny, distinctly glaucous above, and with rounded, obtuse, or emarginate apices. Plants of this kind with glabrous petioles and young branchlets are var. *texensis* (Watson) Rose (Edwards Plateau and north-central Texas to the Arbuckle Mountains of Oklahoma) and those with densely woolly-tomentose petioles and branchlets, var. *mexicana* (Rose) Hopkins (Crockett and Val Verde counties, Texas, to the Trans-Pecos and northeastern Mexico) (cf. Turner). The species is particularly variable in the Arbuckle Mountains and north-central Texas. Edgar Anderson thought this variability to be

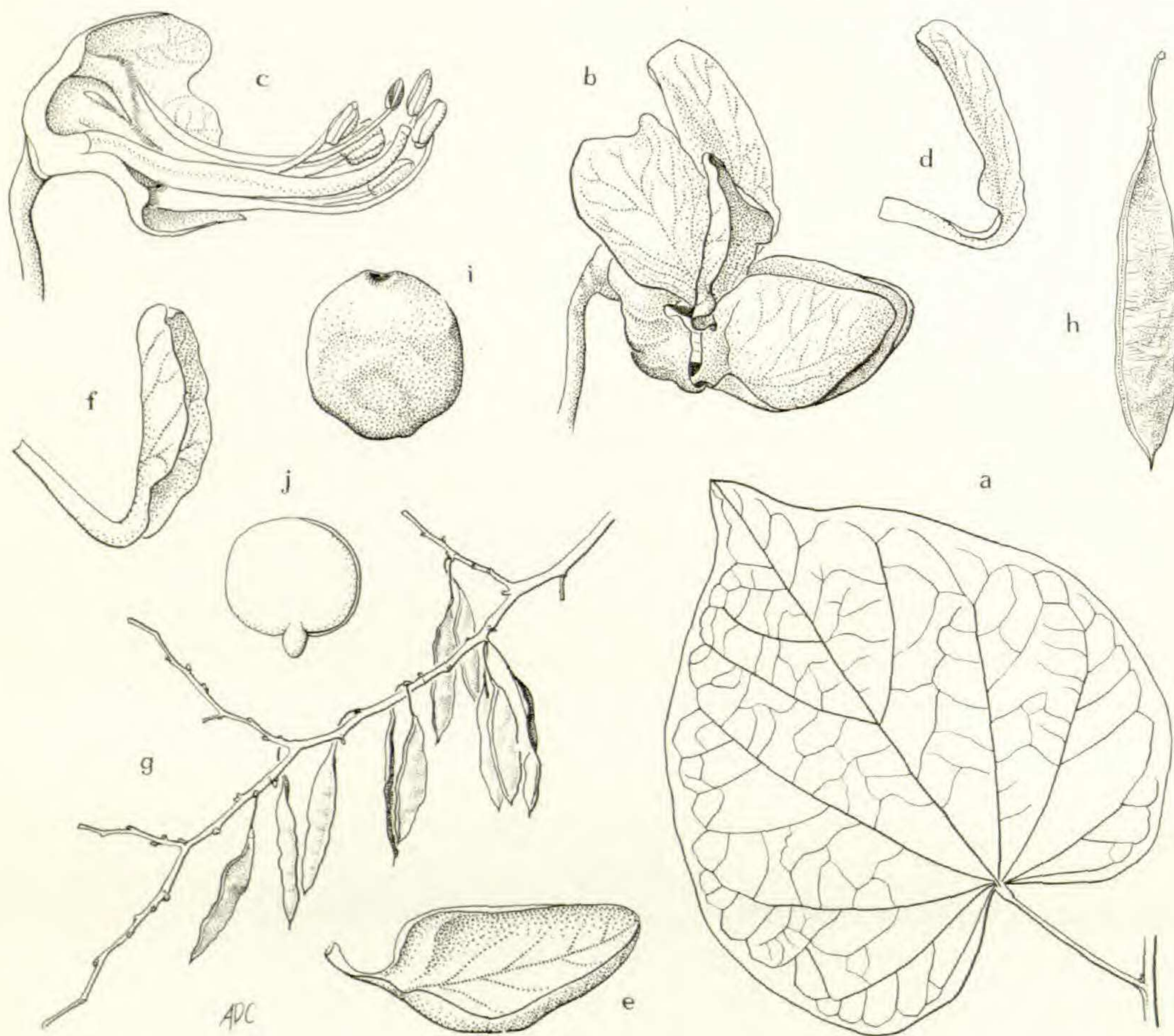


FIGURE 6. *Cercis*. a-j, *C. canadensis* var. *canadensis*: a, leaf — note pulvinus at apex of petiole, $\times \frac{1}{2}$; b, flower, upper banner petal is innermost, $\times 3$; c, flower in partial section, petals removed, 6 stamens shown — note gynophore of gynoecium adnate to floral cup, $\times 4$; d, wing petal, $\times 3$; e, keel petal, $\times 3$; f, banner petal, $\times 3$; g, branch with fruits after fall of leaves, $\times \frac{1}{4}$; h, fruit, $\times \frac{1}{2}$; i, seed, $\times 4$; j, embryo from soaked seed, $\times 3$.

the result of introgression between the typical variety and varieties of the Southwest.

Cercis canadensis var. *canadensis* is most often seen as a small tree, but mature specimens can be moderate-sized trees with broad, rather flat-topped crowns, and the largest recorded plants are more than 16 m. tall, with a crown spread of 13 m. and a trunk diameter at breast height of 0.8 m. (For a photograph of a large specimen, see Plummer & Lindsey.) Redbud is one of the earliest woody plants to flower, and it is in spring, when the plants are in full bloom, that the abundance of this species in much of the eastern United States is apparent. The flowers are papilionaceous in appearance (but the banner petal is innermost). They are borne in sessile umbel-like clusters along the naked growth of the previous year and on older branches and are pollinated mostly by various long- and short-tongued bees. Older trees are especially cauliflorous, and large areas of the trunk can be covered by inflorescences. Flowering begins before the leaves expand, and the flowering period seems longer than it really is, since the magenta floral tubes are conspicuous for some time before the lavender-pink petals open. Varietas *canadensis* has a rather wide tolerance of environmental conditions, although it prefers strong sunlight and soils that have good drainage and are derived from limestone or sandstone. In the northern and eastern part of its range, it is found in open woodlands, borders of woods, thickets, limestone glades and openings, and along rocky streams and bluffs. Toward the south and west, it occurs in rich woods, ravines, bottomlands, and rich soil along streams. Varietas *canadensis* and var. *texensis* are evidently ecologically separated in the region where their distributions overlap, with the former occurring on sandy soils and the latter on calcareous soils.

Eastern redbud and flowering dogwood, *Cornus florida*, have similar geographical distributions and often occur together (perhaps even in some localities in Mexico). Although redbud is usually nearly past flowering when the dogwood begins to bloom, in exceptional years both are simultaneously in full flower, producing a spectacular show of spring color. In some localities redbud flowers at about the same time as some of the shadbushes (*Amelanchier*) and wild plums (species of *Prunus* sect. PRUNOCERASUS).

The fruits of *Cercis canadensis* are strongly flattened and persist on the plants until after the leaves have fallen. They are evidently dispersed by wind blowing them off the branches at various intervals during the fall and winter. Late in the season, while the fruits are still on the plants or after they have fallen, the sutures open on some of the fruits, releasing the seeds; in the case of those fruits that do not open, seed release is effected by the decay of the fruit wall.

Cercis canadensis var. *canadensis* is commonly cultivated in temperate regions and is hardy considerably north of its natural range. White-flowered plants, f. *alba* Rehder, are becoming common in cultivation, and plants with rather unsightly double flowers, f. *plena* Sudworth ex Schneider, are also known. Several cultivars, with the flowers a paler color than

usual, have been named. The eastern redbud does not grow very well in England and southern Europe, where the true Judas tree, *C. Siliquastrum*, is commonly cultivated and extensively naturalized. It is said that the Judas tree, both in cultivation and in the wild, produces a show of spring flowering as spectacular as that of our eastern redbud; this species does not do well in our climate and is rarely cultivated here. *Cercis occidentalis* and *C. canadensis* vars. *texensis* and *mexicana* are seldom cultivated outside the areas in which they occur naturally. The Chinese redbud, *C. chinensis*, is occasionally cultivated in eastern North America and is hardy at least as far north as Boston. Ernest Wilson considered *C. racemosa* to be one of the very best and most beautiful of the flowering trees introduced by him into cultivation, but it is rarely grown in North America and is not hardy northward. Bean says that there are a few living plants in England. (The other Chinese species are evidently not in cultivation in North America.)

Cercis is a very distinctive genus within the Caesalpinioideae. Because of the "simple" leaves that are actually derived from the fusion of two leaflets (see Fries), the gamosepalous calyx with valvate calyx lobes, the ten free stamens, and the dorsifixed anthers that open by longitudinal slits, *Cercis* is grouped with *Bauhinia* L. sensu lato in tribe Cercideae. Several species of *Bauhinia* are commonly cultivated in southern Florida, but none are known to escape.

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